May 2021 • Volume 11, No. 3

ANIMAL FRONTIERS The review magazine of animal agriculture

Animal Domestication: From Distant Past to Current Development

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Animal Frontiers is published in 6 issues by the American Society of Animal Science (ASAS), Canadian Society of Animal Science (CSAS), the European Federation of Animal Science (EAAP), the American Meat Science Association (AMSA), the World Association for Animal Production (WAAP) and a rotating guest society. This magazine synthesizes information, through applied reviews, from across disciplines within the animal sciences. *Animal Frontiers* is provided as a benefit to the members of these societies.

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Guest Editors, Thomas Cucchi, Muséum national d'Histoire naturelle/CNRS, Paris, France; Benjamen Arbuckle, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA.

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ISSN 2160-6056 (print) ISSN 2160-6064 (online)

About the cover. Animal Domestication:From Distant Past to Current Development

"Waterscape domestication" in Amazonia.

HTTPS://DOI.ORG/10.1093/af/vfab019

People can change plant and animal populations by managing and interacting with them and their environment; this process is known as domestication. While most studies on domestication focus on terrestrial environments, Indigenous forest peoples in Amazonia have also managed landscapes using the water when available.

Because the classical concept of domestication does not precisely capture the ways in which forest peoples envision, relate to and modify the aquatic environment, **the authors propose the concept waterscape domestication to describe human-waterscape interactions in the Amazon**.



Examples of waterscape domestication in Amazonia include:



The concept of waterscape domestication is more inclusive of Indigenous cosmologies and better describes human interactions with Amazonia waterscapes. **Further collaborative efforts with local Indigenous people will help to address conservation challenges, focusing on waters, wetlands, aquatic animals, and fisheries management.**

Infographic "Waterscape domestication" in Amazonia.

Animal domestication was a pivotal point in human history and coincided with a major change in human evolution. The domestication of crops was quickly followed by the domestication of livestock (Cucchi and Arbuckle, 2021). While a major focus of this Animal Frontiers issue is on the origins of domestication, current adaptations to domestication to meet challenges of environmental sustainability (Prestes-Carneiro et al., 2021) and to feeding human populations (Lecoq and Tomey, 2021) are also explored.

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- Prestes-Carneiro, G., R. Sá Leitão Barboza, M. Sá Leitão Barboza, C. de Paula Moraes, and P. Bearez. 2021. Waterscapes domestication: an alternative approach for interactions among humans, animals, and aquatic environments in Amazonia across time. Anim. Front. 11(3):92–103.

Lecoq, T. and Toomey L. 2021. A workflow to design new directed domestication programs to move forward current and future insect production. Anim. Front. 11(3):69–77.

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Introduction Letter from the World Association for Animal Production

Philippe Chemineau

President WAAP, Hoover, AL, USA

Corresponding author: chemineau@waap.it

This issue of *Animal Frontiers* on Animal Domestication is the first to be overseen by the World Association of Animal Production (WAAP). It marks the entry of this federation into the consortium that owns *Animal Frontiers* magazine. I would like to thank here the founding members of the consortium, in particular ASAS and EAAP, for welcoming us, thereby showing a common desire to give this magazine a more global dimension and to contribute to maintaining the high quality of articles published there for more than 10 yr.

This magazine aims to be an interface between the world of science and its users, whether they are decision-makers, teachers, technicians, students, and even researchers in the animal sciences sector or in neighboring sectors.

WAAP, like the other members, will be responsible for one annual issue of the magazine. This is a sign that we are now confronted, as scientists interested and committed in animal sciences, with global problems that will have to be dealt with at the places where they arise through active collaboration not only between countries, but also between continents.

The climate emergency is here, the collapse of biodiversity in a large part of the globe is now a reality, the pressure on natural environments has never been so strong and, at the same time, we must feed in a healthy way and economically accessible, an ever-growing population. Like other human activities, agriculture, and in this context animal agriculture, contributes to a portion of these man-made disorders of the modern era. The latter is currently accused of all the evils in the matter of climate change and loss of biodiversity. However, animal agriculture can also be part of the solution by participating in the resolution of climate, biodiversity, and food crises. How to produce better while reducing its carbon impact? How to develop farming systems that protect biodiversity? What diets based on animal products should be promoted for better health?

We will not be able to answer these questions by remaining isolated in our respective countries. We need to exchange and exchange again, first the ideas and then the results of our

About the Author



Philippe Chemineau is initially an Agronomist. He has a PhD in Reproductive physiology of domestic animals. He is Emeritus Director of Research INRAE (France) and President World Association of Animal Production (WAAP). He has been Head of the INRAE Division Animal Physiology Livestock and Systems; Member of national INRAE Management Board; Head of the « Delegation for scientific expertise, Foresight and Advanced studies (DEPE)" INRAE Paris; Head of the INRAE "Direction of Regional

policy, Higher education and Europe (DARESE)". He has also been President of EAAP (European Association of Animal Production), the European Federation of Animal Science.

He has published 196 publications and has an h-index: 38.

research, leading finally to the innovations to enable us to answer the questions presented above. Although the current pandemic is not very favorable, it will also be necessary to encourage networking interactions among men and women who are involved in the animal sciences, so that this community gets to know one another and thereby increases our collective scientific and technical effectiveness.

Animal Frontiers is one of the tools that allows this flow of information and WAAP is the global network of Animal Science associations that wants to promote exchanges between its members. Current members of the Animal Frontiers Consortium understand and share this strategy and therefore we wish to thank them for giving us the opportunity to serve as a partner in this Consortium.

I am proud and happy that this first issue, which presents the history of animal domestications in the Neolithic and later, is the crucible of this rapprochement between *Animal Frontiers* and our federation.

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Introduction

Animal domestication: from distant past to current development and issues

Thomas Cucchi[†] and Benjamin Arbuckle[‡]

[†]Département Homme et Environnement, Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements, UMR 7209, Muséum national d'Histoire naturelle/CNRS, Paris, France

[‡]Department of Anthropology, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA

Domestic animals have played an important role in shaping human Evolution and History. After millennia of constructing niches based on hunting, gathering, and foraging, a range of communities in diverse parts of the world embarked on trajectories of food production which in some instances led to the emergence of complex societies, urbanism, and empires, sowing the seeds for our current globalization. Thanks to intensive zooarcheology and genomics research, it is now common knowledge that, apart from dog domestication within hunter-gatherers societies around 23,000 years Before Present (BP) terminus post quem (Perri et al., 2021), the domestication of globally important livestock animals occurred within sedentary communities engaged in early agriculture in three independent cradles. The oldest of these is located in Southwest Asia where cereals (wheat, barley), legumes (pulse, peas, lentils), and fruits (figs) were domesticated between 12,000 and 10,000 BP, followed by sheep, goat, pigs, and cattle between 10,500 and 10,000 BP (Colledge et al., 2013). The second cradle is located in China where domesticated millets and rice were cultivated in the Yellow and Yangtze River valleys by 10,000 BP. This was followed relatively rapidly by pig domestication in the Yellow River valley (Jing and Flad, 2002; Cucchi et al., 2016). The last major center of ungulate domestication is located in the Andes, where agriculture based on imported maize and locally domesticated potato, beans, and squashes emerged between 9000 and 8000 BP along with South American camelids, llamas and alpacas, later followed by Barba's duck and the guinea pig around 4000 BP (Pearsall, 2008; Hardigan et al., 2017). North America, also contributed to global animal domestication with the turkey by 2000 BP (Speller et al., 2010). In the Old World, a later series of animal domestications focused on the use of animal labor, with the domestic forms of donkey, horse, and camel emerging between 5000 and 2000 BP (Clutton-Brock, 2014). These animals revolutionized human economies and transportation, boosting the power of states, empires and the scale of warfare. Domestic animals have continued to emerge in recent times, including the rabbit in medieval Western Europe, rodents (including rats and hamsters) in the 19th and 20th centuries, as well as the fast-growing field of fish domestication in the 21st century.

Searching for the origin of food production through plant and animal domestication has been a central preoccupation of prehistorians since the mid-20th century (Boyd, 2017), with narratives focusing on themes of technological progress, intentionality and human mastery over their environment (Childe, 1946). These perspectives are firmly anchored in a western anthropocentrism characterized by a strong nature/culture dualism and are still strongly embedded in the archeological literature (Hodder, 1990). However, since the 1980s, anthropologists have emphasized perspectives beyond western ontologies (Descola, 2005) providing ethnographic examples in which distinctions between wild and domestic, culture and nature are minor or even nonexistent (Ingold, 1996). The field of zooarcheology has therefore moved away from earlier narratives emphasizing animal domestication as human domination over nonhuman animals toward a focus on the ecological, cultural, and coevolutionary relationships that have always existed between humans and nonhumans and their intensification and elaboration in the contexts of early farming societies (Vigne, 2015).

Zooarcheology has struggled to find an approach that can take into account the vast range of human-nonhuman interaction and the biological and social components encompassed by the concept of domestication (Russell, 2002). From the biological side, some scholars have focused on domestication as an evolutionary process, drawing inspiration from the work of Darwin (1868). This perspective focuses on the role of intentional human selection in driving the evolution of domestic animals (Clutton-Brock, 1994) or on the consequences (both intentional and unintentional) of human niche construction (Zeder, 2016). The biological side can also focus on the mutualistic/symbiotic relationships between humans and nonhuman animals (Zeuner, 1963; O'Connor, 1997), emphasizing the active role of nonhuman animals in these relationships (Orton, 2010). From a social perspective, scholars emphasize the continuum of relationships between human and nonhuman animals by

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rejecting a simple wild/domestic dichotomy and focusing instead on the role of human intentionality in bringing animals into the cultural sphere where they become incorporated into the human social world (Jarman et al., 1976; Hecker, 1982). Recently, Zeder (2012) has used the concept of domestication pathways as a synthesis of biological and social components of domestication. In this comprehensive approach, evolutionary process, mutualism, and human intentionality are mobilized to propose three pathways for animal domestication: the commensal pathway, the predation pathway, and the directed pathway. This model has provided a useful framework to explore the domestication process in archeology. More recently, the powerful conceptual framework of Niche Construction Theory has been mobilized to further bridge the social and biological views on animal domestication and provide new insights into the coevolution of human and nonhuman societies (Zeder, 2016). To merge social with biological views and tackle the full complexity of animal domestication, a systemic socioecological approach of the interaction dynamics between of human and nonhuman societies has also been proposed (Vigne, 2015).

In addition to the theoretical framing of domestication, the when and why of early animal domestication continues to be debated. Dating the beginning of animal and plant domestication relies on the recognition of observable modifications of the morphologies of seeds and animal bones from archeological sites, testifying to the occurrence of plants and animals already transformed by an ongoing domestication process. But long before this "proper" domestication, we find that by 12,000 BP, in Southwest Asia, evidence that human populations were modifying the landscape to facilitate the growth of local wild plants by tilling and tending cultivated fields, several thousand years before clear evidence of morphological changes were found in the archeological record (Hillman et al., 2000). This form of management predating morphological changes is sometimes referred to as "pre-domestic cultivation" and emphasizes that genetic changes in target populations must predate their first appearance in the archeological record (Willcox, 2012). Such management of the landscape has been a key component of the economies of the people of the Amazonian floodplain, creating an anthropogenic forest and waterscape to secure plant and animal resources (Clement et al., 2015). For animals, hunters have long been interfering with their environment to facilitate and sustain their access to valuable animal resources (both alimentary and symbolic) by selectively hunting and fishing, managing streams to promote spawning, transplanting animals to populate islands devoid of game, and raising juveniles. In light of these practices, it is clear that close relationships including management and cohabitation between humans and animals began long before the appearance of "domestic" forms and should be explored in the broader scope of the domestication of the environment (Scott, 2017). The efficient cognitive apprehension by hunters societies of their environment (Lévi-Strauss, 1962) suggest that animal domestication was not a cognitive revolution but rather a response by some assemblages of human-animal pairings to socioecological conditions conducive to intensification. The example of dog domestication, which has been dated through ancient genomics to the late Pleistocene, proves that this intensification could happen in a wide range of socioeconomic conditions not limited to sedentary farming.

Since the Neolithic (referred to by some as the start of the Anthropocene), animal domestication represents a major shift in the influence of humanity over their life on earth and ultimately over humanity's future. One of the key components of the "sixth extinction" of animal species which we are facing is the tremendous biomass reached by domestic animals (Barnosky, 2008). The impact of domestic animals on current ecosystems and their massive consumption of resources is more obvious when we consider that two thirds of the terrestrial vertebrate biomass on earth is made of domestic animals; humans representing the other third while wild animals only represent 3% to 5% of this terrestrial biomass, demonstrating how humans and livestock have dramatically transformed the biosphere since the advent of animal and plant domestication (Smil, 2003). Virtually all extant megafaunal species are currently under threat and if, as seems likely, they go extinct, the largest terrestrial mammal in the coming centuries will be cattle (Smith et al., 2018). Along with the global presence of herding animals, since the 19th century the number of new small animals kept as pets and incorporated into global supply chains represents a huge threat for the biodiversity and human health. These new pets include newly domesticated mammals (e.g., golden hamster, chinchilla) and birds (budgerigar, parakeet) as well as species of wild mammals, fishes, reptiles, arthropods, and birds which are directly collected from their natural habitat to feed an exponentially growing global pet market. These species can be vectors of zoonosis but can also be potentially invasive, threatening autochthonous wildlife in addition to the ecological damage brought by the trapping and catching of popular (especially tropical) species. The future of animal domestication is now facing a huge challenge ahead. The human population is projected to reach 10 billion in 2050 according to OECD. The evergrowing desire for animal protein also fostered by globalization and the spread of affluent consumer economies will not be met by the current unsustainable agroeconomic model (Smil, 2001). Fish and insect domestication could be a part of the solution, although the challenges are numerous.

Included in this issue of *Animal Frontiers* are eight review and two perspective articles showcasing the long-lasting history of animal domestication, the challenging task to document its origin in the archeological record and its latest development to face the challenge of food production. The first review takes us to Brazil, where Gabriela Prestes Carneiro from UFOPA in Brazil and colleagues from UFPA and from the Natural Museum of Paris in France, propose a concept of "Waterscape domestication" to capture the management and husbandry of aquatic animals by forest people and the time depth of these practices in the Amazonian floodplain (Prestes-Carneiro et al., 2021). The next four reviews provide the latest understanding on the origin of five emblematic domestic animals. Dr Benjamin Arbuckle and Theo Kassebaum from the University of North Carolina propose a rethinking of the origins of cattle management in Southwest Asia, hypothesizing that intensification in human-cattle relationships may have occurred within many early farming communities

of the Fertile Crescent, long before domestic forms of cattle are evident in the archeological record (Arbuckle and Kassebaum, 2021). Dr Daniel Fuks from the University of Cambridge and Dr Nimrod Marom from the University of Haifa explore the long-term relationship between humans, sheep, and wheat which has its origins in Southwest Asia but which, they argue, is reflective of a long process of globalization (Fuks and Marom, 2021). Dr Hitomi Hongo and Hiroki Kikuchi from Tokyo University and Hiroo Nasu of Okayama University describe divergent pathways of early pig management in the Yellow River and Yangtze valleys in China, linking processes of pig management to local environmental conditions as well as agricultural systems based on millet in the north and rice in the south (Hongo and Kikuchi, 2021). Dr Hugo Yacobaccio from the University of Buenos Aires provides a review of the archeological evidence for the still elusive South American camelid domestication process (Yacobaccio, 2021). Finally, Dr Masaki Eda from the Hokkaido University in Japan tracks the genomic and archeological evidence of chicken domestication in Southeast Asia (Eda, 2021). The next two reviews provide an insight into the many trajectories and complexity of potential pathways toward animal domestication. Dr Andrew Somerville from Iowa State University and Dr Nawa Sugiyama from the University of California, Riverside provide an example of a discontinuous domestication relationship. Focusing on cottontail rabbits in the Americas, the authors describe clear evidence for intensive rabbit management at the ancient city of Teotihuacan but propose behavioral barriers inherent to the species as well as cultural factors to explain the ultimate failure to produce a long-term domestic leporid population (Sommerville and Sugivama, 2021). Dr Ardern Hulme-Beaman from Liverpool University and colleagues from York University and the Natural History Museum of Paris provide new insights into the poorly understood history of the brown rat, proposing different steps in the domestication trajectory of this rodent, from a commensal species in Neolithic China to a laboratory model animal and a popular new pet (Hulme-Beaman et al., 2021). This special issue finishes with two perspectives on the ongoing process of animal domestication to face the challenges of feeding the 21st century human population with animal protein in a sustainable way. Dr Fabrice Teletchea from the University of Lorraine in France provides the latest understanding of the fast-growing process of fish domestication and proposes the application of a directed domestication pathway on local fish species to avoid future failure and foster sustainability (Teletchea, 2021). Finally, Dr Thomas Lecoq and Dr Lola Toomey from the University of Lorraine in France propose a program workflow built on the accumulated knowledge of animal domestication to develop the future of insect domestication (Lecoq and Toomey, 2021). Together, the papers in this volume provide a picture of the past, present, and future of animal domestication and emphasize the immense impact of this phenomenon on both human history and global ecology.

About the Authors



Thomas Cucchi received its PhD from the Natural History Museum of Paris in 2005. He is a zooarcheologist whose research focuses on the origins, spread, and evolution of anthropogenic species over the last 15,000 years. Using an integrated approach associating zooarcheological studies with the latest development in morphometric and molecular studies, he has published on animal domestication, commensalism, and dispersal in South Western Asia, China, Island South East Asia, and Europe. He is currently working on new methodological approaches of early process of animal do-

mestication in archeology, using functional plasticity in bone morphology and epigenetic markers. **Corresponding author: cucchi@MNHN.FR**

Benjamin Arbuckle received his PhD from the Department of Anthropology at Harvard University in 2006. He is an archeologist whose research focuses on the prehistory of Southwest Asia and the intersection and human and nonhuman animals in human history. He has published on the



early domestication of livestock in the Neolithic of SW Asia as well as the rise of pastoral lifeways in later periods. He is currently working on projects exploring the history of horse hunting and husbandry in ancient Turkey as well as on the history of wool.

Conflict of interest statement. The authors declare no conflict of interest.

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Feature Article

Management and domestication of cattle (Bos taurus) in Neolithic Southwest Asia

Benjamin S. Arbuckle and Theo M. Kassebaum

Department of Anthropology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599, USA

Implications

- The traditional narrative that taurine cattle domestication occurred 8500 BC in the Euphrates valley, Syria is critiqued.
- Domestic cattle are argued to appear later than widely acknowledged in a wide area of Southwest Asia.
- The "pre-domestic management" of cattle preceded the appearance of a domestic phenotype perhaps prior to 8500 BC.
- Pre-domestic cattle management as well as early morphologically domestic cattle likely emerged in multiple regions of Southwest Asia rather than in one center.

Key words: animal management, aurochs, cattle, domestication, Neolithic Southwest Asia

Introduction

Cattle are one of the most significant animal partners in human history, and the origins of cattle management as well as domestic cattle have been the focus of scholarly interest for decades (Peake and Fleure, 1927; Reed, 1960). Here, we assess evidence for the management and domestication of taurine cattle (Bos taurus Linnaeus 1758) in prehistoric Southwest (SW) Asia focusing on archaeological and ancient DNA datasets. Although related, the histories of "cattle management" and "domestic cattle" represent two separate questions. The former refers to a range of techniques including penning, foddering, dairying, mate selection, and selective culling which may vary in intensity, whereas the latter describes biological changes associated with human husbandry, reproductive isolation from progenitors, and selection pressures within an anthropogenic environment (e.g., Dyson, 1953).

doi: 10.1093/af/vfab015

The dominant narrative describing cattle domestication places its origin within the early farming settlements of the Fertile Crescent region of SW Asia dating to the ninth millennium BC (a period known as the Early Pre-Pottery Neolithic B [PPNB]) (Figure 1; Table 1). However, we argue that this narrative is based on models which imagine a single geographic center of innovation and emphasize biometric evidence for body size diminution, i.e., the history of "domestic cattle" rather than "cattle management." We critique this narrative arguing that the appearance of "domestic cattle" in the ninth millennium BC is largely a mirage and that domestic phenotypes in fact appear in the eighth millennium BC. However, the management of cattle must have preceded changes in phenotype and likely emerged a millennium or more earlier across a wide geographic region including much of the northern and southern Levanttemporal and geographic patterns that fit with recent interpretations of the histories of other livestock species (e.g., Zeder and Hesse, 2000; Martin and Edwards, 2013).

Defining Domestic Cattle

Domestic cattle (*B. taurus* Linnaeus 1758) are thought to derive from the extinct aurochs (*Bos primigenius* Bojanus 1827), subspecies of which inhabited a wide range of habitats across Eurasia and North Africa (Zeuner, 1963). Recent genomic research has identified two lineages of domestic cattle: the first represented by taurine cattle whose ancestry is thought to lie primarily in Neolithic SW Asia, and the second by zebu cattle (*Bos indicus*, Linnaeus 1758), which can be traced back to a South Asian population of aurochsen (Verdugo et al., 2019). Here, we focus on the early history of taurine cattle in SW Asia, although it is important to note that by the Bronze Age (c. 2000 BC), taurine and zebu cattle became increasingly hybridized, a situation reflected in many modern cattle populations (Verdugo et al., 2019).

Traditional models for identifying the process of cattle domestication focus on identifying changes in phenotype, especially reduced body size and smaller and more variably shaped horns. These changes in phenotype are part of the "domestication syndrome" and have been defined and used by generations of archaeozoologist to distinguish (small) domestic cattle from (large) wild aurochs at prehistoric sites (Duerst, 1908:360). Demographic data relating to age at death and adult sex ratios have also been used to assess cattle domestication

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Figure 1. Map showing the location of Neolithic sites mentioned in the text. 1. Orman Fidanlığı, 2. Hattuşa, 3. Çadır Höyük, 4. Erbaba, 5. Çatalhöyük, 6. Boncuklu, 7. Acemhöyük, 8. Musular, 9. Aşıklı Höyük, 10. Köşk Höyük, 11. Cafer Höyük, 12. Çayönü Tepesi, 13. Körtik Tepe, 14. Ganj Dareh, 15. Çavi Tarlaşı, 16. Hassek, 17. Nevalı Çori, 18. Gritille, 19. Lidar Höyük, 20. Göbekli Tepe, 21. Gürcütepe II, 22. Mezraa-Teleilat, 23. Tell Halula, 24. Jerf el-Ahmar, 25. Mureybet, 26. Tell Qaramel, 27. Djade al-Mughara, 28. Shillourokambos, 29. Tell Aswad, 30. Qarassa 3, 31. Hagoshrim, 32. Beisamoun, 33. Sha'ar Hagolan, 34. Kfar HaHoresh, 35. Yiftahel, 36. Mishmar Ha-Emeq, 37. Kebara, 38. Gilgal, 39. Jericho, 40. Ain Ghazal, 41. Abu Gosh, 42. Motza, 43. Afridar, 44. Ashkelon, 45. Grar, 46. Beidha, 47. Basta, 48. Ksar Akil, 49. Teleilat Ghassul.

Table 1. Chronological terminology and approximate dates in calibrated years BC

Archaeological period	Calibrated years BC
PN	6800/6300-6000/5500
FPPNB/PPNC	7000–6300
LPPNB	7500-7000
MPPNB	8000-7500
EPPNB	8500-8000
PPNA	9500-8500
Late Epipaleolithic	13000–9500

as have analyses of stable isotopes from bovid teeth exploring changes in diet and weaning associated with cattle husbandry (e.g., Balasse et al., 1997). Ancient DNA studies have also added to our understanding of the histories of cattle providing evidence for admixture between wild and domestic populations (Verdugo et al., 2019).

The Traditional Narrative

The upper Euphrates valley of northern Syria has been presented as the "hearth" of taurine cattle domestication. This process is dated to the mid ninth millennium BC associated with the early farming villages of the PPNB (Table 1) (Helmer et al., 2005; Peters et al., 2005). Here, scholars have uncovered a long tradition of *Bos* exploitation among early sedentary communities in a region where the river valley and adjacent grasslands must have supported a large endemic aurochs population (Figure 1).

The earliest of these sites, Tell Mureybet, provides a sequence of occupation from the late Epipaleolithic to the middle PPNB (**MPPNB**) (Table 1). Helmer and Gourichon (2008) argue that Mureybet's hunters targeted herds of female and juvenile aurochs in the early levels with changes in hunting directed towards increasing production for a growing human population at this large site as well as increased interest in symbolically potent bull aurochs—the remains of which are found in settlements across the region (Cauvin, 1994; Helmer et al., 2004).

Dramatic changes in human cattle relationships are reflected at the site of Dja'de al-Mughara dating to the early PPNB (EPPNB), where Helmer argues morphologically domestic cattle are evident for the first time (Helmer et al., 2005). This is based primarily on a small reduction in the size of "male" cattle as evidenced through mixture analysis of a limited set of measurements. The disruption of "natural" sexual dimorphism is interpreted as the result of human management, particularly selection for nonaggressive males, and is seen as the first step in the morphological divergence of domestic cattle. Although presented cautiously by the authors, this small shift in the biometric properties of "male" Bos forelimbs is widely reported in the secondary literature as the origins of domestic cattle. As a result, "8500 BC, northern Syria" is the answer that will likely be reported if one queries "when were cattle domesticated?" in an online search engine.

Following the appearance of "domestic" cattle in the Euphrates valley, they are reported on the island of Cyprus at the end of the ninth millennium BC (Vigne, 2011b:1072). Scholars have further traced the spread of a domestic cattle phenotype into neighboring regions including Anatolia and SE Europe, the southern Levant, North Africa, Iran, and the Caucasus in a time transgressive pattern. It is frequently stated that cattle husbandry spread slowly within SW Asia only appearing in the mid seventh millennium BC in central Anatolia and Sagros regions (Arbuckle, 2013; Marom and Bar-Oz, 2013; Arbuckle et al., 2016).

This narrative has been incorporated into ancient DNA studies giving it further credence and legitimacy. In a widely cited paper, Bollongino argues that a combination of ancient and modern mitochondrial DNA sequences suggests that as few as 80 female aurochs could have initially been involved in the domestication process which is seen as a geographically and temporally "limited phenomenon" centered in one or two Neolithic villages, such as Dja'de (Bollongino et al., 2012:2103). However, Verdugo et al. (2019) emphasize that later admixtures have fundamentally hidden the early genetic history of cattle including extensive hybridization with zebu cattle from South Asia. Verdugo's analysis perpetuates other aspects of the traditional cattle domestication narrative; however, including the notion that domestic taurine cattle are derived from a "restricted northern Fertile Crescent genetic background" and that phenotype (particularly body size) can be used to distinguish domestic cattle from aurochs (Verdugo et al., 2019:175).

Origins of Domestic Cattle

Despite the success of the Euphrates-EPPNB cattle domestication narrative, we argue that the history of cattle domestication is more complex. Zooarchaeological evidence from the Tigris drainage in southeastern Turkey is particularly important showing an alternative history of cattle domestication in a neighboring region. Here, the site of Çayönü Tepesi provides a time sequence recording changes in *Bos* populations and exploitation from the PPNA through the Pottery Neolithic (**PN**) (Öksüz, 2000; Hongo et al., 2009).

At Cayönü, Bos remains are abundant in the earliest levels (PPNA) representing c. 20% of the mammalian remains and they exhibit large body size and a sex distribution reflecting the targeting of female aurochsen-similar to the situation documented in the early layers of Mureybet. This pattern of exploiting morphologically wild females continues into the EPPNB and Bos remains increase dramatically in the subsequent MPPNB where smaller "domestic" individuals appear for the first time (Hongo et al., 2009). In the following phase, dated to c. 7500 BC, cattle reach their maximum abundance at Çayönü, but are phenotypically identical to the aurochs of the earlier PPNA period. A "permanent" decrease in size is only evident around 7000 BC (late PPNB [LPPNB]) followed by continued decrease in cattle size into the PN (Hongo et al., 2009, figure 1). Moreover, age at death data show wide variability through time but with a notable increase in the culling of juveniles in the LPPNB and PN. Finally, shifts in both C and N isotopes from cattle teeth are evident in the early MPPNB, suggesting changes in Bos diets beginning in the late ninth millennium BC and becoming more apparent in the LPPNB. This combination of datasets presents a complicated picture which is difficult to fit into a simple linear narrative (although see Peters et al., 2017).

In central Anatolia, faunal evidence for Bos exploitation reflects yet another pattern. Although Perkins (1969) argued for early cattle domestication at the Neolithic village of Catalhöyük, subsequent faunal work has described a tradition of aurochs hunting which targeted adult animals and large males, elements of which were sometimes curated within houses (Baird et al., 2018). This focus on large, adult bulls is also evident in the nearby uplands of Cappadocia in the eighth millennium BC (Russell et al., 2005). At Catalhöyük, phenotypically domestic cattle are documented in the mid seventh millennium BC reflecting a curious "delay" in the appearance of domestic cattle in a region with a long tradition of sedentary farming, intensive Bos exploitation, and contact with cattle herding neighbors (Arbuckle, 2013; Russell et al., 2013). Peters et al. (2013, 2017) have hypothesized that prior to the appearance of domesticates, morphologically wild Bos populations at Catalhöyük may have been under human management with herders intentionally maintaining a wild phenotype through regular introgression with bull aurochs.

In the southern Levant, the traditional narrative argues that domestic cattle were a late addition to the animal economies of the region (Horwitz et al., 1999). It is frequently reported that "full domestication" of cattle occurred in the sixth millennium BC (PN) (Marom and Bar-Oz, 2013). However, at Tell Aswad in the Damascus basin, changes in horn morphology and a loss of sexual dimorphism in the MPPNB suggest that "domestic" cattle were present prior to the PN in the southern Levant (Helmer and Gourichon, 2008). Helmer and Gourichon (2008:138) also note the presence of pathologies thought to represent the use of cattle for labor and hypothesize that milk was also exploited in the eighth millennium BC (Helmer et al., 2018). In addition, small-sized "domestic" cattle have been identified at Yiftahel in Israel, and Basta and Ain Ghazal in Jordan dating to the eighth millennium BC (Hecker, 1975; von den Driesch and Wodtke, 1997; Becker, 2002; Sapir-Hen et al., 2016). In their summary of cattle domestication in the southern Levant, Horwitz and Ducos (2005:219) state that cattle "clearly exhibit the morphological and metrical changes associated with domestication" in the eighth millennium BC, and Munro et al. (2018) have recently argued that shifts towards cattle management began as early as the ninth millennium (EPPNB) in the southern Levant, completely erasing the perceived time lag with the Euphrates valley.

Analysis of genetic evidence from ancient cattle in SW Asia raises further questions about the notion of a single center for cattle domestication. Verdugo's important analysis of genomes from 67 ancient bovines shows three divergent Neolithic lineages in SW Asia (Verdugo et al., 2019). Among these, "A" is reflected in the early Neolithic Balkans (but with its origins somewhere in SW Asia); "B" is identified in Neolithic Anatolia and Iran; and "C" is found in the southern Levant. These genetic results suggest that multiple regional populations of aurochsen were incorporated into Neolithic herds, especially north and south of the Taurus, raising questions about the need to center cattle domestication on the northern Fertile Crescent.

Origins of Bos Management

The dominant view of cattle domestication processes focuses on a single center in the Euphrates basin and the emergence of "domestic" forms of cattle in the EPPNB despite questions about the scale of phenotypic changes at this time and evidence for early cattle management in other regions of SW Asia. In contrast, the idea that animal management preceded morphological changes and was geographically widespread has been at the core of work exploring the origins of the management of other livestock taxa for decades. These ideas are relevant for our understanding of the history of cattle as well.

Intensive regimes of "pre-domestic" animal management (i.e., management without clear morphological changes) have been documented for livestock progenitor species across the Fertile Crescent region in the early Holocene. At Ganj Dareh in Iran and Aşıklı Höyük in central Anatolia, evidence for selective culling patterns, foddering, and onsite penning and use of animal dung indicates that morphologically wild sheep and goats were intensely managed in the ninth millennium BC (Zeder and Hesse, 2000; Stiner et al., 2014). These practices persisted for centuries and are not isolated. Similar arguments for the early management of morphologically wild ungulates have been made across SW Asia (e.g., Hecker, 1975; Horwitz, 2003; Vigne, 2011a). These management strategies predating morphological changes have been variously described by scholars as incipient domestication, cultural control, proto-elévage, proto-domestication, and pre-domestic management (Hecker, 1975; Vigne et al., 2000; Munro et al., 2018).

Models of pre-domestic animal management are therefore not new and have even been previously applied to cattle. At Tell Mureybet, Ducos (1978) described evidence for management but no reduction in body size in the EPPNB occupation as a system of *proto-elévage* reflecting the husbandry of morphologically wild animals. Scholars working in central Anatolia, the Euphrates basin, the southern Levant, and Cyprus have all suggested that morphologically wild cattle were managed for centuries prior to the appearance of morphological features of the domestic syndrome (Ducos, 1978; Monahan, 2000; Sana and Tornero, 2013; Munro et al., 2018). The hypothesis of local cattle domestication in regions outside of the Euphrates, including Jordan, the Upper Tigris, and North Africa, has also been explored (Becker, 2002; Marshall and Hildebrand, 2002; Munro et al., 2018).

Thus, an alternate model of pre-domestic cattle management, not limited to a single geographic center and not tied to changes in phenotype, has been available for decades. We argue that this model fits the zooarchaeological and genetic data well. Moreover, analysis of ancient genomes for goats, pigs, and cattle suggests that wild populations from multiple regions of SW Asia contributed to domestic herds reflecting a geographically de-centered domestication process. This is more in line with recent views of the domestication process which tend to emphasize its centerlessness and mosaic nature (Goring-Morris and Belfer-Cohen, 2011) as well as the decoupling of morphological changes from management (Zeder and Hesse, 2000).

One of the problems associated with identifying the appearance of domestic cattle is confusion regarding "how small is small enough" to be considered "domestic"? Although Helmer et al. (2005:90) argue that the individuals from EPPNB Dja'de and MPPNB Halula "are clearly smaller" than the aurochs from earlier sites, the decreases in mean size are very small (Helmer et al., 2005: table 1); a similar situation is evident for the cattle from Shillourokambos (Vigne, 2011b:1070). Moreover, for Saña and Tornero (2013:291), "clearly domestic" (i.e., small sized) cattle are only present at Halula in the early PN (c. seventh millennium BC) rather than the MPPNB. Similar arguments have been echoed at Mezraa-Teleilat (Ilgezdi, 2008) and Gritille (Monahan, 2000) on the Turkish Euphrates and are also widely expressed in the southern Levant (Marom and Bar-Oz, 2013) perhaps reflecting different expectations in regards to the scale of size diminution associated with domestication.

However, when we look at summaries of biometric data representing long time sequences in the Euphrates basin, central Anatolia, and the southern Levant, we can see broad patterns of change over time within their regional context (Figure 2). Biometric data are presented using the Log Size Index (LSI) which compares archaeological measurements against those of a standard animal—in this case, a cow aurochs from the Mesolithic site of Ullerslev, Denmark (Meadow, 1999; Steppan, 2001). Values above "0" reflect dimensions larger than those of the standard while negative values are smaller. In Figure 3, we have generated mean values for "male" and "female" *Bos* using mixture analysis in order to further assess the nature of size change in this sexually dimorphic species.

In Figure 2, we use the interquartile range of the LSI values for aurochs from Mureybet (I–III) to model the size parameters for a SW Asian aurochs population. For the Euphrates region,



Figure 2. Summaries of biometric data for prehistoric *Bos* from sites in SW Asia presented using LSI. Boxplots of LSI data for selected sites from (A) the Euphrates valley (including Shillourokambos, Cyprus); (B) central Anatolia; and (C) the southern Levant. Horizontal lines represent the interquartile range for LSI measurements from Mureybet (I–III). Arrows indicate earliest significant decrease in size (analysis of variance Tukeys pairwise test P < 0.05). EBA, Early Bronze Age; EC, Early Chalcolithic; LBA, Late Bronze Age; LC, Late Chalcolithic; MBA, Middle Bronze Age; MC, Middle Chalcolithic. Sample size in parentheses. See Supplementary Material for data references.

the earliest large-scale reduction in size, evident as the LSI median moves below the interquartile range of the Mureybet aurochs, is at MPPNB Mezraa-Teleilat on the Turkish Euphrates dating to the early-mid eighth millennium BC (Figure 2A). Despite arguments that early "domestic" cattle phenotypes were established in the EPPNB at Dja'de and Shillourokambos, Cyprus, these populations are broadly similar to the morphologically wild cattle from PPNA Mureybet, Jerf el-Ahmar, Göbekli Tepe, and the Natufian southern Levant (also see Figure 3). Body size continues to decline at Mezraa-Teleilat in the LPPNB and into the PN. However, inter-site variability persists with much larger cattle (including both "males" and "females" [Figure 3]) present at PPNB Mureybet and LPPNB Gürcütepe compared to contemporary sites in the Euphrates valley (Figure 2). Rather than reaching a stable "domestic phenotype" in the Neolithic, body size continues to change over time with dramatic declines and wide variability evident in the late Chalcolithic and Bronze Age.

In Central Anatolia, LSI values for *Bos* at eighth millennium Aşıklı and Musular are comparable in size to Euphrates aurochs, and, at Çatalhöyük, the largest "male" and "female" sizes are evident in the early seventh millennium BC (Figures 2B and 3). Although a decline in body size clearly takes place in the mid seventh millennium in this region, variability is again evident with cattle from contemporaneous Early Chalcolithic (EC) Çatalhöyük and Köşk Höyük displaying very different LSI profiles and diminution continuing into the Chalcolithic and Bronze Age.

In the southern Levant (Figure 2C), Bos remains from Epipaleolithic, PPNA, EPPNB, and MPPNB sites are broadly comparable in size to Euphrates aurochs-with "male" and "female" LSI means from MPPNB Mishmar Ha-Emeq very similar to those from PPNA Jerf el-Ahmar (Figure 3). Notably smaller cattle appear at some MPPNB sites including Yiftahel and Basta, where both "male" and "female" mean values drop (Figure 3). Kfar HaHoresh, a mortuary site in Israel where cattle feature in feasting practices, includes material from the LPPNB which explains the presence of small-sized cattle at this site otherwise dominated by large aurochs-sized Bos dating to the EPPNB (Meier et al., 2016). More dramatic declines in size in the southern Levant are evident in the seventh millennium (PPNC) and in the PN, where "male" and "female" means continue to decline (Figure 3). In the Chalcolithic and Bronze Age, size declines precipitously but also exhibits significant heterogeneity.

These broad biometric summaries show three important features of the temporal and geographic patterns of size change



Figure 3. Mean LSI values for both "male" (\mathfrak{O}) and "female" (\mathfrak{Q}) *Bos* from the Euphrates valley (blue) (Shillourokambos, Cyprus included), central Anatolia (red), and the southern Levant (purple) based on mixture analysis (Past v3.20). Sites labeled as in Figure 1.

in SW Asian *Bos* which add to our understanding of cattle domestication processes. First, the size change argued to represent early domestication in the EPPNB is subtle to the point of being unobservable using LSI transformed measurements. Although Vigne (2011b:1068) notes that size diminution in the EPPNB is only weakly expressed, and primarily as a disruption in sexual dimorphism, this point has largely been lost in the secondary literature where "domestic cattle" are regularly reported as originating in the ninth millennium BC. Second, large-scale decreases in body size are apparent in the Euphrates valley only in the eighth millennium BC when they also begin to appear in the southern Levant. Third, body size continues to change dramatically in later periods emphasizing that managed cattle are characterized by phenotypic variability in all periods.

These biometric patterns indicate that body size is a dynamic variable which has temporal and geographic dimensions not clearly linked to categories of wild versus domestic. In their careful study of the cattle from Tell Aswad, Helmer and Gourichon (2008:136) warn that body size is not a good criterion for distinguishing wild and domestic cattle and that large size does not necessarily equate to a wild animal, thereby recognizing the problems of conflating phenotype with management (also Helmer et al., 2018:85).

From current archaeological data, we are able to answer the question "when do phenotypically domestic cattle appear in the archaeological record"? Significant changes in body size and horn shape are documented in the eighth millennium BC (MPPNB) in the Upper Euphrates valley, the Upper Tigris valley, and in the Damascus basin. This correlates with regionwide increases in caprine pastoralism, agricultural productivity, and inter-regional connectivity (although not homogenization) taking place within the so-called PPNB "interaction sphere" (Arbuckle and Atici 2013; Borrell and Molist 2014). However, if we decouple phenotype from management, we are left with the question "when and where did cattle management emerge"?

Early sedentary food-producing communities of the Fertile Crescent were centers of "experimental" pre-domestic animal management practices at least as early as the ninth millennium BC (Arbuckle and Atici, 2013; Peters et al., 2017; Munro et al., 2018). Moreover, morphologically wild cattle were transported to Cyprus by the end of the ninth millennium BC providing a *terminus ante quem* for pre-domestic cattle management. This leads us to hypothesize that early cattle management was practiced in a variety of forms in early sedentary villages dating to the 10th and early 9th millennia BC (PPNA and EPPNB) and perhaps even extending back into the Younger Dryas (11th millennium BC). Geographically, we hypothesize that diverse, local management traditions emerged in multiple contemporary communities in the upper Euphrates and Tigris valleys, the Jordan Valley, Mediterranean coast, and central Anatolia.

Likely candidates for loci of early management include sites such as Mureybet, Qarassa 3, and Tell Qaramel in Syria, and Göbekli Tepe, Körtik Tepe, and Boncuklu in Anatolia where aurochs remains are abundant (Arbuckle and Özkaya, 2007; Gourichon and Helmer, 2008; Ibañez et al., 2010; Grezak, 2012; Baird et al., 2018). At Mureybet, Ducos (1978) suggested that morphologically wild cattle were under human management in the EPPNB. It seems likely that at least some of the morphologically wild cattle at Mureybet were subject to a suite of management strategies in earlier periods as well. Moreover, at Göbekli Tepe in southeastern Turkey, Peters et al. (2013:97) noted that the demographic profile for *Bos* suggests "deliberate manipulation" of this population in the PPNA, suggesting that pre-domestic management may have been among the exploitation techniques applied to aurochs at this site. In central Anatolia, it has been argued that aurochs were hunted prior to the appearance of domestic phenotypes in the mid seventh millennium BC (Russell et al., 2005; Arbuckle, 2013; Pawłowska, 2020). However, given the symbolic, social, and economic importance of cattle in the region, it is plausible that aurochs were subject to forms of management including penning, foddering, and selective culling in the earliest levels of Çatalhöyük, and perhaps at earlier sites in the region such as Boncuklu.

If, as we hypothesize, pre-domestic cattle management was practiced in villages of the PPNA and EPPNB across the Fertile Crescent, why do phenotypic changes only become evident in the eighth millennium? We suggest that the answer is related to the nature of pre-domestic management regimes which may have been small in scale, discontinuously applied, and may not have involved the population isolation necessary to accumulate phenotypic changes associated with the domestication syndrome.

As Vigne (2009:157) points out, the earliest management strategies probably included a constellation of techniques representing just a portion of the diverse forms of interaction between humans and aurochs. We expect that the scale of *Bos* management was small at its inception and may have been applied intermittently. It was therefore a complement to, rather than a replacement for, the hunting of aurochs which continued in the region long after the emergence of domestic cattle.

Peters et al. (2015) have argued that the domestication process involved a long period of "learning by doing" involving inevitable failures and initial low success rates—a feature evident in the range of techniques applied to early caprine management and the ultimate failure of cattle management on Neolithic Cyprus (Vigne 2011b; Arbuckle and Atici, 2013; Stiner et al., 2014). Low success rates in raising aurochs in captivity may have necessitated constant restocking from local free-living populations, a feature seen in pre-domestic caprine management which effectively limited the development of domestic phenotypes.

Moreover, it is likely that the goals of early animal management taking place in the context of a hunting economy were not the same as those in later periods. In particular, an emphasis on large males for feasting and display is suggested by demographic profiles at many sites, as well as practices including the caching of cattle remains (especially bucrania) and imagery of bulls, which are evident across SW Asia from the 10th through the early 7th millennia BC (Cauvin, 1994; Helmer et al., 2004). A central goal of pre-domestic herd managers may have been to provide visually impressive animals for socially and cosmologically charged events. These goals may have been met with intermittent bursts of management and frequent recruitment from free ranging populations specifically designed to maintain wild phenotypes.

If cattle were managed in PPNA and EPPNB villages, as we hypothesize, what management techniques were applied to pre-domestic livestock and how do we identify them if they coexisted with hunting techniques? Surprisingly, the practices of early cattle management have not been addressed in recent scholarship but were a lively topic in the past. For example, Peake and Fleur (1927) present a model of incipient cattle domestication in their influential summary of prehistory. The authors suggest the earliest stage of cattle domestication involved the capture, penning, and foddering of a small number of pregnant cow aurochsen (Peake and Fleure, 1927:34). Through a combination of provisioning and familiarization, aurochs cows and their calves became acclimatized to their resourcerich "home." Allowing cows and calves to graze and return to pens at night would ensure seasonal opportunities to mate with free-living male aurochs. Although more than a century old, this model has the benefit of accommodating the behavioral difficulties of living in close proximity to adult, male aurochsen as well as describing a plausible scenario in which small-scale management regimes which inhibit morphological changes could be applied. Although cattle penning deposits have not been specifically identified in Neolithic SW Asia, it has been suggested based on isotopic evidence that morphologically wild cattle at Kfar HaHoresh were foddered and perhaps penned (Makarewicz et al., 2016).

The symbolic importance of aurochs within PPNA settlements has been widely noted (Cauvin, 1994; Helmer et al., 2004). Although the potent symbolism associated with the largest prey species in SW Asia has been identified as a potential factor in the late domestication of cattle (Vigne, 2009:157; Arbuckle, 2013), the opposite may be true. It may be that the social and cosmological significance of aurochs drove the efforts to capture, pen, and fodder them and also contributed to the slow shift to a domestic phenotype (Peters et al., 2013). The latter may have been intentionally delayed, especially in central Anatolia, where impressive physical appearance seems to have been highly valued.

The types of pre-domestic management strategies hypothesized for the 10th and 9th millennia BC, particularly when situated within a mosaic of other exploitation techniques, pose serious challenges in terms of identification and require a renewed and explicit research focus. Exploring the diets and mobility of individual cattle through isotopic analyses and changes in the skeleton associated with penning may provide indicators of human impact on individual animals (e.g., Zimmermann et al., 2018; Harbers et al., 2020). Studies of ancient cattle genomes may identify the movement of specific lineages such as those brought to Cyprus, further elucidate the origins of domestic cattle within local aurochs populations, or identify phenotypic changes related to human selection such as coat color not evident in the skeletal record. Finally, geomorphological evidence for onsite penning has clarified the early history of sheep and goat management (Stiner et al., 2014; Matthews, 2016; Portillo et al., 2020), and similar evidence for offsite cattle penning may allow us to further tease out the details of evolving human-Bos relationships in early sedentary communities.

Conclusion

The traditional narrative that domestic taurine cattle originated in a few villages in the upper Euphrates valley in northern Syria in the EPPNB is problematic. We argue that this narrative is a mirage based on inconsistent interpretations of biometric evidence for size change and geographically centered models of domestication. Instead, dramatic changes in cattle phenotype including body and horn size are evident in a wide arc including the Upper Euphrates, Upper Tigris, and southern Levant almost a thousand years later (eighth millennium BC).

The breakwater points widely identified as the origins of domestic taurine cattle—the EPPNB in Euphrates and its chronological equivalent on Cyprus, the PPNC or PN in the Jordan Valley, and the PN in central Anatolia—are recognized as important inflection points in human–cattle relationships, notably the widespread appearance of new domestic phenotypes, but they do not represent the beginning of close relationships between humans and aurochs which extend temporally in both directions. Rather, we argue that a long history of predomestic cattle management preceded the appearance of "domestic" cattle, whose slow reproductive rates, combined with early herders "learning by doing," and an apparent preference for the "aurochs aesthetic" likely made it necessary for herders to draw from local aurochs populations thereby inhibiting the appearance of domestic phenotypes.

Instead of focusing on the Euphrates valley in the mid ninth millennium BC, we hypothesize that early cattle management was practiced in many sedentary communities of the PPNA across the Fertile Crescent region. Idiosyncratic and heterogenous systems of *proto-elévage* or pre-domestic management must have emerged in the centuries if not millennia prior to the EPPNB in communities such as Mureybet and Göbekli Tepe as well as contemporary settlements in the Jordan valley and Mediterranean coast where relationships of hunting slowly transformed into management and management, combined with population isolation, eventually transformed aurochs into cattle. Through the concentration of a suite of high-resolution analyses of archaeological and archaeogenetic material in these periods and places, we predict scholars in the next decade will produce a new chapter in the history of taurine cattle extending out of the Euphrates valley, past evidence for size change, and temporally beyond the PPNB.

Supplementary Data

Supplementary data are available at Animal Frontiers online.

Acknowledgments

The authors wish to express their gratitude to two anonymous reviewers for their comments on an earlier version of this manuscript. Financial support for some of the work presented in this paper was provided by National Geographic Society, the American Research Institute in Turkey, National Science Foundation grants (BCS-0530699 and BCS-1311551), Encyclopedia of Life Computable Data Challenge, Baylor University, and UNC Chapel Hill. The authors are indebted to Joris Peters, Nadja Pöllath, and Hijlke Buitenhuis for

About the Authors



Benjamin S. Arbuckle is Associate Professor in the Department of Anthropology at the University of North Carolina at Chapel Hill, USA. He received a PhD in Anthropology from Harvard University with a thesis focused on sheep and goat pastoralism in prehistoric Anatolia. Research

interests include the origins of domestic livestock, zooarchaeology, and prehistory of SW Asia especially Turkey. **Corresponding author:** bsarbu@email.unc.edu

Theo M. Kassebaum is a doctoral candidate in the Department of Anthropology at the University of North Carolina at Chapel Hill, USA. She received an MSc degree in Zooarchaeology from the University of York, UK and a BA in Anthropology from the University of Chicago. Research interests focus around economic resilience and animal management in times of environmental and political unrest especially in Bronze Age SW Asia.



collaborations and sharing data. Faunal work at Köşk Höyük, Acemhöyük, and Çadır Höyük was carried out with the support of Prof. Dr. A. Öztan and Dr. G. McMahon and with the permission of the Turkish Ministry of Culture and Tourism.

Conflict of interest statement. None declared.

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Feature Article

Sheep and wheat domestication in southwest Asia: a meta-trajectory of intensification and loss

Daniel Fuks^{1,‡,} and Nimrod Marom^{||,}

[†]McDonald Institute for Archaeological Research, Department of Archaeology, University of Cambridge, Downing St, Cambridge CB2 3ER, UK

^{*}Martin (Szusz) Department of Land of Israel Studies and Archaeology, Bar-Ilan University, Ramat Gan 5290002, Israel [®]Department of Maritime Civilizations and the Leon Recanati Institute for Maritime Studies, University of Haifa, Haifa 3498837, Israel

Implications

- Biologists since Darwin considered domestication a model for the study of evolution; we argue that domestication may also be a model for the study of globalization.
- The long-term history of wheat and sheep domestication exemplifies the intensification of relationships between humans and a small number of species native to southwest Asia, which includes long-term globalizing processes.
- Specific indicators are offered for tracking the longterm globalization of sheep and wheat, with reference to production intensity, geographic diffusion, and diversity.

Key words: agricultural diversity, globalization, Neolithic package, origins of agriculture, pastoralism

Introduction

Domestication as here understood is one outcome of human-environment interactions whereby certain plants and animals undergo genetic changes resulting from their close relationship with humans, including increasing reliance on humans for survival and reproductive success. Domestication is thus an ongoing process and may be viewed as part of an even broader process of intensification in the relationships between humans and certain plants and animals, including hunting/gathering, herding/cultivating, specialized agriculture/

doi: 10.1093/af/vfab010

pastoralism, and, recently, genetic engineering. It should be emphasized that these are not stages in a necessarily directional process, but these categories do represent a scale of intensification, at least in the strict agricultural sense of more plant/ animal product per unit land (Harris, 1989). Domestication has enhanced evolutionary fitness for domesticated species, humans included (Rindos, 1984). It is thus a type of symbiosis, the study of which contributes to broader understandings of evolution (Ladizinsky, 1998; Larson et al., 2014). In the case of wheat and sheep, symbiotic relationships developed not only between sheep-humans and wheat-humans but also between wheat-sheep, especially as a result of intensified management strategies, for example, grazing on stubble in harvested fields, foddering and manuring, and forest clearing. As has long been appreciated, these relationships involve biological and cultural aspects (e.g., Rindos, 1984; Ingold, 1996).

Whereas the tradition of studying domestication as a model for evolution goes back to Darwin, we argue that domestication research also offers a model for the study of globalization. This suggestion ensues from the insight that several components of the meta-trajectory outlined below as intensifying relationships between humans, wheat, and sheep, are manifest in many other ongoing economic, social, and ecological processes. These can be broadly summarized as "globalization" in the widely accepted sense of intensifying worldwide interconnectedness, including in economic, cultural, political, and environmental spheres (Held et al., 1999: 2). Our long-term history of sheep and wheat domestication agrees with the consensus view that contemporary globalization represents new levels of intensification, but also that it has much earlier roots than is commonly acknowledged. Finally, we offer specific indicators for tracking the long-term globalization of sheep and wheat domestication, with reference to production intensity, geographic diffusion, and diversity.

Sheep

Sheep are the second most abundant ruminant livestock animal after cattle (Gilbert et al., 2018) and have been bred intensively to optimize wool, milk, fat, or meat production. In

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southwest Asia, sheep were among the first domesticated livestock. Together with goats, cattle, and swine, they make up the key animal components of the Neolithic "package," which subsequently spread throughout the globe (Figure 1). Sheep were domesticated from the mouflon (*Ovis orientalis*), with little evidence for genetic input of other wild congenerics (*O. vignei*, *O. nivalis*, *O. ammon*) to extant or archaeological populations (Deng et al., 2020). Domesticated sheep have descended from several mouflon lineages, suggesting a complex population history (Pedrosa et al., 2005).

The date of first appearance of sheep in Cyprus at ca. 8000 BCE (Vigne et al., 2011) is a solid terminus ante quem for management, as sheep are not part of the native Pleistocene fauna of this island and so must have been introduced there. It is more difficult to pinpoint the somewhat earlier intensification within the Pleistocene range of mouflon in southwest Asia. Early evidence for domestication is found in the reduction of caprine body size in sites from the upper Euphrates basin (Nevalı Çori) in the mid-9th millennium BCE (Peters et al., 2005). A broadly similar date has been obtained from Aşıklı Höyük in Anatolia (Stiner et al., 2014). From this cradle of domestication in southwest Asia, sheep spread across Anatolia (Arbuckle, 2008), to the southern Levant in the 8th millennium BCE (Horwitz et al., 1999), to Crete by 7000 BCE (Jarman and Jarman, 1968), to the Greek mainland by 6500 BCE (Davis and Simões, 2020), and to the Iberian peninsula and the Maghreb by ca. 5500 BCE (Kandoussi et al., 2020; Figure 1). By 4000 BCE sheep were present in northern Europe (Rowley-Conwy, 2013). The earlier 5th millennium BCE also witnessed the first appearance of domesticated sheep in China (Dodson et al., 2014). Sheep and other domestic livestock first appear in Africa by 5000 BCE (Muigai and Hanotte, 2013), reaching the inner, southern, and western parts of the continent appreciably later, in the 1st and 2nd millennia BCE (Marshall and Hildebrand, 2002).

The transition from hunting to domestication of sheep has tracked multiple paths during the southwest Asian Neolithic (Makarewicz, 2013). Different combinations of herding, hunting, and farming were tried-not all of them successful or sustainable-as revealed by the archaeological record. For example, nondiscriminant early slaughter of animals from both sexes, against modern utilitarian logic, appears in Aşıklı Höyük (Stiner et al., 2014); slaughter of younger males seems to have become a widespread management tactic only by the end of the 8th millennium BCE (Arbuckle and Atici, 2013). Foddering has been suggested in Neolithic southern Jordan (Makarewicz and Tuross, 2012) and Anatolia (Miller and Marston, 2012), while manipulation of lambing season has been identified in Neolithic France, 5th millennium BCE (Tornero et al., 2020). Mosaics of agricultural and transhumant practices are found across southwest Asia (Martin, 1999; Arbuckle and Hammer, 2019). The first evidence for vertical transhumance between mountains and plains appears in 6th millennium BCE Anatolia (Makarewicz et al., 2017).

Another element of pastoral complexity concerns choices regarding which domestic species to raise and in what proportions, giving rise to an endless variety of possibilities evident in the diversity of pastoralists' herding strategies. For instance, a manifold range of considerations determines the logic behind the ratio between the two caprine species in traditional southwest Asian herding strategies (Redding, 1981; Cribb, 1984). In general, sheep products (meat, milk, wool) are considered more valuable than those of goats in southwest Asia, but sheep require more water, more herbaceous pasture, and therefore larger ranges. Goats have fewer dietary and water requirements, breed faster, and are more suitable as livestock for the risk-averse or when human and land resources are limited. The complexity of early domestication processes is echoed in the multiple pathways through which livestock, among them



Figure 1. Long-term diffusion of domesticated sheep and wheat from their centers of origin. Schematic portrayal of the spread of domesticated sheep (brown) and wheat (yellow) across Eurasia and beyond, with approximate dates of arrival in key areas. Insert shows approximate phytogeographic distribution of wild progenitors, wild mouflon sheep (*Ovis orientalis*) in brown and wild emmer wheat (*T. turgidum* subsp. *dicoccoides*) in yellow.

sheep, were integrated into subsistence practices in different regions of the world. Whereas in Europe they were part and parcel of the agricultural package that spread westward and northward from southwest Asia, in Africa a slower process of assimilation appears to have been the rule (Zeder, 2017).

The utilization of secondary products such as milk and wool (Sherratt, 1983) has been an important consideration for keeping sheep throughout history. There is evidence for the use of sheep's milk already in Neolithic diets (Hendy et al., 2018), as another strategy for obtaining dietary value. Wool, however, is a newer currency through which long-range social debts can be committed: it represents an ability to harness marginal lands for the production of tradeable goods, which support a complex economic structure (McCorriston, 1997). The development of specialized breeds for wool production is suggested to have occurred for the first time in late 4th millennium BCE Mesopotamia (Algaze, 2009), based on iconographic representations of coil-horned rams with fleeces, which replaced a large corkscrew-horned breed. Significantly, this change can be traced in the biometry of sheep in the region (Vila and Helmer, 2014). Large-scale wool production, alongside other types of specialized herding (e.g., fat-tailed sheep for food and sacrifice), is associated with the late 3rd millennium BCE Ur III state (Stepien, 1996) and is known in southwest Asia and the eastern Mediterranean throughout the 2nd-1st millennia BCE (Killen, 1964). Specialized breeding further intensified under subsequent empires, such as those of the Assyrian, Classical, and Islamic worlds (Davis, 2008; Marom and Herrmann, 2014).

Recent centuries have seen a revolution in the domestication relations between sheep and humans. The mesta system of Merino shepherding in medieval Spain and the British wool industry associated with the bursting international trade of the industrial revolution, exemplify intensification in the context of early capitalistic growth (Klein, 1920). In modern times, this process continues in the modern Australian Merino fiber industry, exemplifying new levels of agropastoral intensification in the historical process of globalization. Here a former British colony utilizes a North African breed to supply diverse markets worldwide, including that of Olympic sports. Scientific advances in selective breeding over the last 200 years, and its increasing efficiency due to artificial insemination within the context of factory farming, has caused a sharp decline in genetic diversity relative to population size (estimated at ~1.2 billion sheep worldwide). The effective population size of many breeds is now below 50, local breeds have disappeared, and the cultural diversity associated with pastoral production is dwindling. Following the genetic cloning of Dolly in 1997, the conceptual path to intrusive genetic intervention in sheep breeding was laid. Today, CRISPR/Cas9 edited Australian Merino sheep that can produce both fine wool and quality meat represent the materialization of this path (Crispo et al., 2015), topping an already mounting concern for the genetic future of sheep due to diversity loss (Taberlet et al., 2011).

Wheat

Wheat is the most important source of food grain for humans today and the largest primary commodity (FAO, 2014). Although wild wheats are native only to southwest Asia, domesticated wheat has spread throughout the globe (Figure 1). Today, wheat fields occupy more land than any other crop on the planet (FAO, 2014, 2020), representing an extreme case of domestication and diffusion. "Wheat" refers to a genus of grasses (*Triticum*). A natural classification system groups wheat species by chromosomal ploidy (multiples of distinct sets of chromosomes) and combinations of distinct genomes (Table 1; van Slageren, 1994; Zohary et al., 2012: 23–9; Haas et al. 2019). Wheat subspecies are further differentiated as wild/ domesticated and hulled/free-threshing and by number of kernels per spikelet—genetic traits that have clear phenotypic expressions in wheat spikelet morphology (Hillman et al., 1996).

The key trait distinguishing wild and domesticated cereals is spikelet brittleness. In wild cereals, the spikelet acts as a dispersal unit, disarticulating from the ear at maturity, dispersing by different vectors, and implanting itself in the ground with the aid of its awns (Figure 2). Spontaneous disarticulation upon maturity-which leaves a smooth scar on the rachis segmentmakes it difficult to harvest fully ripe wild cereals from the ear, although a small percentage (ca. 10%) of nonbrittle spikelets are retained at the base of wild cereal ears (Kisley, 1989). Prior to domestication, Epipaleolithic people, ca. 21–9.7 ka Cal BCE, gathered wild wheat, among other grasses (Weiss et al., 2004; Arranz-Otaegui et al., 2018a), for grinding and food preparation (Nadel et al., 2012; Arranz-Otaegui et al., 2018b), and may have even engaged in cultivation of wild cereals (Snir et al., 2015). Growing archeobotanical evidence suggests predomestication cultivation of wheat and other grasses in the PPNA, 9.7-8.8 ka Cal BCE (Weiss et al., 2006; cf. Abbo et al., 2021).

In domesticated cereals, the spikelet no longer acts as a dispersal unit and does not disarticulate upon ripening. For dispersal and germination, domesticated wheat relies on planting by humans. The tough rachis segments may separate by tearing at the internodes, leaving rough scars (Figure 2).

Table 1	. Natural	classification	n of wheat	species	(after
Zohary	et al., 20	12, Table 3)			

Ploidy	Genomes	Species name	Wild/domestic forms
Diploid (2n)	AA	Triticum monococcum L.	Wild & domestic
Diploid (2n)	AA	T. urartu Tuman	Wild
Tetraploid (4n)	BBAA	T. turgidum L.	Wild & domestic
Tetraploid (4n)	GGAA	T. timopheevii Zhuk.	Wild & domestic
Hexaploid (6n)	BBAADD	T. aestivum L.	Domestic
Hexaploid (6n)	GGAAAA	T. zhukovskyi Men. & Er.	Domestic

Increasing proportions of rachis segments with rough scars in archeobotanical assemblages place initial domestication of emmer and einkorn wheat in the EPPNB, 8.8–8.3 ka Cal BCE, proliferating in the MPPNB, 8.3–7.7 ka Cal BCE, throughout southwest Asia (Zohary et al., 2012: 36–38, 41–43; Arranz-Otaegui et al., 2018a). However, archeobotanical data suggest that it took some 2000 yr between initial domestication as represented by >20% nonbrittle rachises and full morphological domestication of >80% domestic rachises (Fuller et al., 2018; cf. Abbo et al., 2021). Over the same period, increased kernel breadth is an additional marker of domestication (Fuller et al., 2018).

The first domesticated wheats were, like their wild progenitors, "hulled" or "glume" wheats, meaning that their kernels are tightly enclosed in the spikelet by tough glumes that do not break off during threshing and which therefore require dehusking to release the kernels (Figure 3). In addition to einkorn and emmer, an apparently distinct domestication of Timopheev's wheat (Table 2) is indicated by a recent archeogenetic study identifying as such the extinct "new glume wheat" known from the Neolithic archeobotanical record in Anatolia and the Balkans (Czajkowska et al., 2020). New glume wheat was cultivated for millennia before its extinction, but other forms of domesticated Timopheev's wheat are extant (Jones et al., 2000).

"Free-threshing" or "naked" wheat kernels are surrounded by thinner glumes, which release the kernels upon threshing, as in tetraploid durum wheat and hexaploid bread wheat (Figure 3). Free threshing makes postharvest processing more efficient and was selected for relatively rapidly following initial domestication, as is evident from the Middle/ Late PPNB (Hillman et al., 1996; Zohary et al. 2012: p. 24). Kislev described an early and now extinct form of freethreshing tetraploid wheat, T. turgidum subsp. parvicoccum Kislev, which may have been an intermediary subspecies in the evolution of durum from emmer (Kislev, 1979, 2009; cf. Nesbitt, 2001). Free-threshing wheats replace hulled wheats in Early Bronze Age (ca. 3300-2100 BCE) Anatolia and northern Syria; the same occurred in Late Bronze Age (ca. 1550-1200 BCE) Canaan, although hulled wheats did not phase out entirely and they continued to dominate in the Aegean into the Iron Age (ca. 1200-600 BCE) (Riehl and Nesbitt, 2003; Frumin et al., 2019). Despite their greater processing costs and generally lower gluten content, hulled wheats' persistence is probably due to their greater resistance to poor soil conditions, fungal diseases, and insect pests (Nesbitt and Samuel, 1996).

Another major milestone in wheat domestication is the advent of hexaploid wheat by the 7th millennium BCE (Bogaard, 2016), from spontaneous hybridization of tetraploid domesticated emmer with the diploid wild grass, *Aegilops tauschii* Coss. (Zohary et al., 2012: 33, 47). The latter contributed the D genome, conferring greater adaptability to non-Mediterranean climates (Zohary et al., 2012: 49). Although not exclusive to hexaploid wheats, the evolution of spring wheat, especially via flowering time adaptability to diverse temperatures, soil moisture, and

day length (Kamran et al., 2014), further contributed to their widespread diffusion. Free-threshing hexaploid wheat formed a part of Neolithic farming in Europe by the 3rd millennium BCE (Nesbitt, 2001), while also spreading eastward to India by 2500 BCE, and central China by 2000 BCE, as well as wider latitudes and higher altitudes of Eurasia (Liu et al., 2017). Hulled hexaploid wheats, like spelt, became important to many local economies in Europe from the Bronze Age to premodern times (Nesbitt, 2001, 2005).

By the end of the southwest Asian Neolithic, all the major wheat types described above were under cultivation in Eurasia, with wide inter-regional diversity (Fuller et al., 2018). Domesticated emmer wheat (along with barley) became a staple of the Early Bronze Age Levantine city-states (e.g., Hopf, 1983), although its cultivation in some early agricultural settlements of the period was unsustainable and unsuccessful (White et al., 2014). Among later empires, in 7th c. BCE Assyrian Israel a regional production strategy apparently involved wheat grown in Judea to feed residents of Ashkelon, freeing land closer to the ports for Mediterraneanexport viticulture (Faust and Weiss, 2005). The globalizing Hellenistic-Roman economies apparently effected a transition from hulled emmer to free-threshing durum wheat in their Egyptian breadbasket during the first few centuries CE (Cappers, 2016).

Hulled wheats (at all ploidy levels) gradually phased out of cultivation for their lesser value to commercialized and globalized economies of antiquity and modern times, particularly in tandem with 20th-century globalization of free-threshing hexaploid bread wheat cultivation (Nesbitt and Samuel, 1996). Hulled wheats survived under cultivation in mountainous pockets of western Eurasia, making a minor comeback as popular health foods in recent decades (Nesbitt and Samuel, 1996; Nesbitt, 2005). Today, tetraploid free-threshing durum, or "macaroni wheat," accounts for some 5% global wheat production-much of which is grown in the Mediterranean basin (Royo et al., 2017). Hexaploid free-threshing "bread wheat" accounts for almost 95% of global production and is cultivated in nearly every country worldwide. Aside from enhanced adaptability, hexaploid free-threshing wheat's commercial dominance is due to higher gluten content, making it the ideal bread wheat. Both bread wheat and durum are subject to the full efforts of modern crop improvement, including genetic engineering.

Discussion

A powerful combination of southwest Asian plant and animal domesticates emerged in the Neolithic—an "agricultural package"—of which wheat and sheep are exemplary. Increasing evidence suggests that even after initial domestication, cultivation and livestock rearing developed by numerous and diverse pathways, including much trial and error (White et al., 2014; Honeychurch and Makarewicz, 2016). Although agriculture and pastoralism involve a significant focus on select few species compared with the many dozens utilized by



Figure 2. Domesticated vs. wild wheat. The primary distinction between wild and domesticated wheats is based on spikelet morphology. In wild wheats, spikelets act as dispersal units, disarticulating upon maturity, and leaving a smooth scar on the rachis segment (right). In domesticated wheats, spikelets are released only upon threshing; detachment of spikelets from the spike leaves a rough scar on the rachis fragment (left). Unlike wild wheats, domesticated wheats rely on humans for dispersal and seeding.



Figure 3. Hulled vs. free-thresing wheat. Domesticated wheats are either hulled or free-threshing. In hulled wheats (left), kernels are tightly enclosed in their glumes such that threshing results in intact spikelets. To release the kernels, they must be dehusked. Of the resultant chaff, spikelet forks are a tell-tale identifier of hulled wheats, commonly found in archeobotanical assemblages. In free-threshing wheats, threshing alone is sufficient to release kernels and chaff, which includes rachises indicative of free-threshing wheats.

Subspecies	Wild/domesticated	Hulled/naked	Common name
T. monococcum L. subsp. aegilopoides (Link) Thell.	Wild	Hulled	Wild einkorn
T. monococcum L. subsp. monococcum	Domesticated	Hulled	Domesticated einkorn
T. turgidum L. subsp. dicoccoides (Asch. & Graebn) Thell.	Wild	Hulled	Wild emmer
T. turgidum L. subsp. dicoccum (Schrank) Thell.	Domesticated	Hulled	Domesticated emmer
T. turgidum L. subsp. durum (Schrank) Thell.	Domesticated	Naked	Durum, aka macaroni/hard wheat
T. timopheevii Zhuk. subsp. armeniacum (Jakubz.) van Slageren	Wild	Hulled	Wild Timopheev's wheat
T. timopheevii Zhuk. subsp. timopheevii	Domesticated	Hulled	Domesticated Timopheev's wheat
T. aestivum L. subsp. spelta (L.) Thell.	Domesticated	Hulled	Spelt
T. aestivum L. subsp. aestivum	Domesticated	Naked	Bread wheat
T. zhukovskyi Men. & Er.	Domesticated	Hulled	Zhukovsky's wheat



Figure 4. Population and diversity following domestication. Schematic portrayal of changes in domesticated sheep and wheat population and diversity over time.

hunter-gatherers, the success of southwest Asian food production may nonetheless be attributed to different forms of diversity inherent in the Neolithic package.

The most basic form of such diversity is that deriving from the combination of plants and animals. This not only provides a source of dietary diversity, as does hunting and gathering, but also an added level of risk management associated with agropastoral storage. Whereas wheat grains, among other cereals and legumes, can be stored in permanent settlements for food and sowing, sheep and other livestock are a highly mobile source of food and capital. Together, the combination of stationary and mobile storage provides a wide range of adaptations to environmental anomalies mediated by diverse cultural modes. The development of specialized nomadic pastoralism is a kind of intersociety adaptation on this theme, developed to maximize landscape exploitation by focusing grazing on regions less suitable for agriculture. This perspective is supported by the high degrees of interdependence between specialized pastoralists and farmers, alongside tensions over scarce land and sociocultural differences. Much of later southwest Asian history can be written in terms of these relationships and differences, following the lead of Ibn Khaldun (1958 [1377]). However, it is important to emphasize that rather than a simple binary nomadic pastoralist/sedentary farmer dichotomy, these categories represent continuous spectra with potentially infinite combinations and interrelations.

A different type of diversity contributing to agropastoral buffering capacity involves the set of trade-offs between sheep and wheat vis-à-vis their respective counterparts, goats and barley. Both sheep and goats provide meat, milk, and hides; both wheat and barley provide kernels for food and fodder, as well as chaff and straw for fodder, kindling, building, and other crafts. However, while offering essentially the same products, each member of the pair has slightly different ecological needs and adaptive qualities, with barley and goats generally representing the hardier counterparts to the higher-valued products of sheep and wheat among most ancient and modern southwest Asian cultures. These differences may be exploited in various ways and circumstances, including risk management. For example, droughttolerant barley often succeeds where wheat crops fail, while slightly different ripening times between wheat and barley in southwest Asia offer a buffer against subseasonal precipitation anomalies.

In addition to interkingdom and intergenus diversity just discussed, intragenus and intraspecies diversity presents another gamut of possibilities for economic exploitation, utilized by breeders for millennia. For instance, changes under domestication to seasonal cyclicity in reproduction, involving flowering time adaptations for wheat and multiple lambing seasons in sheep, were key to their global diffusion. Just as genetic diversity has influenced the globalization of sheep and wheat, human socioeconomic globalization has affected their genetic diversity. The spread of these species to diverse and often remote regions catalyzed the development of numerous breeds and varieties (via selection for locally adapted traits, cultural preferences, genetic bottlenecking, etc.), creating a global force for increased intraspecies diversity—a diversity which most people throughout history were unaware of. Contemporary globalization has made this agriculturally significant diversity uniquely accessible in theory, as through gene banks, while causing declining diversity of cultivated/herded stock in practice as landraces become marginalized and extinct. These two countercurrents epitomize contemporary globalization generally: increased awareness of global diversity thanks to heightened connectivity between disparate regions on the one hand, and increased uniformity in cultural, social, and economic spheres on the other hand. If globalization widely conceived is a stage in the intensification of economic, cultural, political, and environmental interconnectedness, the globalization of sheep and wheat is a stage in domestication and agropastoral intensification, the tracking of which may broaden our understanding of contemporary globalization. We propose the following indicators for sheep and wheat intensification with relevance to long-term globalization:

(1) Sheep:goat and wheat:barley ratio

Centralized and market-oriented production appear to favor both wheat and sheep vis-à-vis barley and goats, as well as specific varieties/breeds of each. By the Early Bronze age, wheat and sheep were involved in increasingly extractive, landscape-altering human lifeways, which was part and parcel of the rise of urbanism and empires. Whether in Ur III, the Assyrian Levant, or the Roman Mediterranean, local maxima in wheat and sheep production over time attest to heightened societal complexity, defined simply as increasing energetic inputs and problem-solving outputs (Tainter, 1990).

(2) Population density

Increasing population density may occur on highly local and global levels. The former may involve, for example, intensive rearing of large herds in pens, supported by cultivated fodder. The latter includes global population levels of sheep and goats, which in a globalized world correlate with population densities in "core" areas.

(3) Geographical diffusion

The extreme dispersal of wheat and sheep globally (Figure 1) has been used to explain modern Western global economic dominance (Diamond, 1997; cf. Frank and Gills, 1993). To chart this diffusion is to chart what may be the most basic precursor to globalization (Jones et al., 2011; Liu et al., 2019).

- (4) Ratio of species population to number of extant agriculturally significant varieties and breeds. The globalization of wheat and sheep is also associated with increasing uniformity in the varieties and breeds being raised. In post-Neolithic times, this process includes gradual phasing out of einkorn and other hulled wheats, for example, and the global dominance of "bread wheat."
- (5) Geographic distribution of diversity in varieties and breeds. In a complex society as defined above, higher uniformity in varieties and breeds is expected along the major trade routes. Evenness in the geographic spread of rare landraces is expected to be a function of distance from primary economic and sociopolitical conduits.

Each of these indicators relates to three themes that are central also to contemporary globalization: production intensity, geographic diffusion, and diversity. More specifically, indicators (1) and (2) relate directly to production intensity; indicator (3) *is* geographic diffusion; while indicators (4) and (5) are agropastoral expressions of decreased cultural and genetic diversity (schematically portrayed in Figure 4). Thus, while many scholars view domestication

as a model for evolution, domestication also offers a model for globalization. Sheep and wheat domestication exemplify globalization as a long-term historical phenomenon, which includes preference for output over risk aversion, increasing geographic diffusion and population density, as well as increasing awareness of global diversity and its relegation to collections of the past. We emphasize that these are neither continuous, directional, nor inevitable developments, and their integration in our synthesis of wheat and sheep domestication along a linear time progression should not be misunderstood as a 'progress narrative'. The latter may be just as dangerous when applied to globalization as to evolution. The loss of biological and cultural diversity associated with agropastoral intensification spreads along the hyper-connected highways of globalization, as once the agricultural package comprising both taxa spread from southwest Asia across Eurasia through the ecological corridors afforded by the great river valleys. It may be that research into this meta-trajectory of intensification and loss, common to both sheep and wheat, may result in succoring through documentation a meager fraction of that loss for future generations.

About the Authors

Daniel Fuks is an archeobotanist with academic interests in plant domestication and diffusion, ancient agriculture and pastoralism, ancient economic history, and Mediterranean history. He completed his MA and PhD at the Land of Israel Studies and Archaeology Department of Bar-Ilan University, Israel, and is now a British Academy Newton International Fellow at the McDonald Institute for Archaeological Research, University of Cambridge. Corresponding author: df427@ccam.ac.uk





Nimrod Marom is an archeozoologist studying the interactions between animals, humans, and the environment in the Holocene and Late Pleistocene. He is a member of the Department for Maritime Civilizations at the University of Haifa, and PI of the DEADSEA_ECO project funded by the European Research Council.

Acknowledgments

This research was made possible thanks to the Rottenstreich Fellowship of the Israel Council for Higher Education and the Newton International Fellowship of the British Academy (DF). We would like to thank Aya Marck for the illustrations, as well as Suembikya Frumin and the reviewers for helpful comments, which improved the paper. Any errors remain the sole responsibility of the authors.

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Feature Article

Beginning of pig management in Neolithic China: comparison of domestication processes between northern and southern regions

Hitomi Hongo,[†] Hiroki Kikuchi,[†] and Hiroo Nasu[‡]

[†]Graduate University for Advanced Studies, Hayama, Kanagawa, Japan [‡]Okayama University of Science, Okayama, Japan

Implications

- China was one of the centers of the domestication of pigs. Morphological characteristics and pathological evidences found in pig bones excavated from Neolithic sites in the Yellow River Valley in the north, Yangtze River Valley in the south, and in the region between these two major river valleys suggest that management of pigs had begun around 9000 BP, possibly in multiple places in China.
- Dietary analyses using carbon and nitrogen isotopes in the bone collagen of pigs indicate that a small number of pigs with C4 plants in their diet appeared in northern China in the Early Neolithic between 9000 and 7500 BP. Many *Sus* samples of the Middle Neolithic Yangshao Period, when millet cultivation became the dominant form of farming in northern China, show an intake of C4 plants in their diet. Nitrogen isotope ratios were also elevated, suggesting that many pigs received fodder which included both C4 plants and kitchen wastes.
- Sus with enriched nitrogen isotope values were also found among the Early Neolithic samples from the Yangtze Delta sites. Most pigs from the southern sites had a diet dominated by C3 plants even after millets were introduced to the Yangtze River Valley. The pig managements in southern China were more extensive than those in the northern Neolithic sites, probably because of the abundance of wild plants in the vicinity

Key words: China, domestication of millets, isotope analysis, management of pigs, Neolithic

of the settlements that could be used as fodder for pigs. Hunting of wild animal resources also continued.

• In northern China, the human control over the diet and breeding of pigs was more intensive, and hunting of wild pigs was rare. The isotope ratios of *Sus* samples from Huai and Han River Valley sites were variable, suggesting that each site had a versatile strategy in food production.

Introduction

The relationship between humans and wild boar (*Sus scrofa*) in the process of their domestication has been diverse and complex because of the behavioral and dietary flexibility of *Sus*. Several "pathways" to pig domestication have been proposed (Zeder 2012). Variations in management strategies and intensity of human control over behavioral and reproductive aspects of the life history of pigs resulted in the different trajectories of the domestication process that influenced the rate of phenotypic changes associated with domestication. Pigs were domesticated independently in at least two locations of the world: in northern Mesopotamia by c. 10500 Before Present (**BP**) and in China by c. 8000 BP (Price and Hongo 2019).

In China, sedentary communities emerged by around 11000 BP both in the Yellow River Valley in northern China and the Yangtze River Valley in the south (Liu 2005). These settlements provided the setting for the beginning of domestication of pigs, where some wild pigs took advantage of the anthropogenic niche and the "commensal" pathway proposed by Zeder (2012) could have started. The Neolithic cultures in China are grouped according to the two major geographical regions: those in the Yellow River Valley in the north and those in the Yangtze River Valley in the south. Generally, the east-west line between the Qinling Mountains and Huai River is regarded as the border between these two regions. Wild millets were initially exploited in the northern region, where domestic types of millet were attested by 7800 to 7500 BP (see below), then dryland framing of millets became the main form of agriculture from the Middle Neolithic. Rice (Oryza sativa) was the main

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crop in the southern Neolithic, where the domestic form of rice was reported as early as 8000 to 7000 BP at Kuahuqiao 跨湖桥 in the Lower Yangtze delta. Agriculture developed in the form of intensive production of rice in the irrigated paddy-field. In the initial stage of the Neolithic, wild plants and animals occupied a significant portion of food resources in both agricultural zones. By the Middle Neolithic Yangshao Culture period, dry-land farming of millets combined with pig husbandry supplemented by occasional hunting was the typical form of subsistence in the north. In the south, rice-paddy agriculture and pig management were combined with fishing, hunting, collecting of nuts and other plant resources. Increasing interaction between northern and southern Neolithic cultures in the Yangshao Period promoted southward expansion of millet and northward expansion of rice. The development of social complexity and urbanization supported by increased agricultural productivity can be observed in the Late Neolithic Longshan period in both the north and south. In the Longshan Period, crops and domestic animals of West Asian origin, wheat, cattle, sheep and goats were first introduced to northern China. (See Figure 2 for chronology of major Neolithic cultures in China.)

Zooarcheological data suggest different historical trajectories of pig management practice, based on environmental settings in the north and south. In addition to the differences in major crops, the way that animal husbandry practice was integrated in the agricultural economy could be different in the two regions. We propose that pig management developed as part of overall intensification of agriculture in the north incorporated in the effort to increase productivity, while in the south pigs were added to broad-spectrum utilization of both wild and domestic food resources.

In this article, we will examine the different regional trajectories of pig husbandry practices in the course of Neolithic development in China. The sites mentioned in this article are shown in Figure 1 and Table 1. We will review the evidence of domestication of millets in northern China and discuss the timing and process of intensification of pig management in relation to the beginning of agriculture. The evidence of pig management in the Yellow River Valley and the Yangtze River Valley, where rice was the major crop, will be compared based on morphological and isotopic evidence of carbon, nitrogen and strontium analyses. We will also examine the pig husbandry practices in the fertile region between the two major centers of development of Neolithic cultures, along the Huai and Han rivers. This region functioned to connect the northern and southern Neolithic cultures and became the third important center of Neolithic developments in the Middle and Late Neolithic periods.

Morphological Evidence of Pig Domestication in China

Evidence of management of *Sus* in various degrees of intensification are reported from both the Yellow River Valley and Yangtze River Valley Neolithic sites, starting from around 9000 BP. However, we have little information about the hunting strategies of wild *S. scrofa* or the initial stages of management of *Sus* in China. Also lacking are comprehensive data on the regional variation of the size of wild pig populations, that makes it difficult to assess the size reduction of pigs in the early stage of domestication. Metric data of *Sus* excavated from Neolithic sites in both northern and southern China are gradually accumulating that give us some information about the timing and process of domestication of pigs.

Yellow River Valley

The oldest evidence of management of pigs was reported from Jiahu 贾湖, Henan (9000 BP), located at the southern border of the Yellow River valley. Archeologists argued for pig-keeping being practiced at Jiahu based on the pathological characteristics found on their teeth (e.g., rotation of teeth and frequent occurrences of linear enamel hypoplasia [LEH]), as well as the age profile biased toward younger animals (Luo et al. 2008). Geometric morphometric analyses of three mandibular second molars (9000 to 7800 BP) from Jiahu by Cucchi et al. (2011) also suggested that domestic pigs were present at the site as early as 9000 BP in the Cishan/Peiligang Culture period. In the middle Yellow River Valley in Hebei, at Cishan 磁山, a decrease in the mean length of the lower third molar (41.4 mm) in 8000 BP compared with Paleolithic wild boar (45 mm) was presented as evidence for the beginning of pig management at the site (Yuan and Flad 2002). The mean length of over 41 mm at Cishan is, however, well within the range of Neolithic wild boar if we use the 37-mm threshold suggested by Cucchi (2016) to separate wild and domestic pigs at Xiawanggang 下王岗 in Henan.

The decrease of tooth size continued after 8000 BP. Wang et al. (2015) compared the breadth and length measurements of lower molar teeth of pigs from sites along the Wei River, located south of the Yellow River. The mean lengths of molars of pigs from Wayaogou 瓦窑沟, Jiangzhai 姜寨 I and II, Quanhucun 泉护村, in the Middle Neolithic, were smaller than that reported for Cishan (summarized in Price and Hongo 2019, Table 5), and a trend of size reduction of the mandibular third molar (M3) through time between 6300 and 3600 BP can be observed. Further shortening of teeth is observed at the Bronze Age site Donglongshan 东龙山 (4000 to 3600 BP) where the mean length of lower M3 was 33 mm, well within the range of domestic pigs. In addition, higher rates of LEH compared with modern wild boar were also reported from these sites (Wang et al. 2015).

Yangtze River Valley

In the lower Yangtze Valley, *Sus* occupied less than 10% of the faunal remains at Kuahuquiao (Peiligang Culture, 8000 to 7000 BP). The possibility of the beginning of pig management was suggested based on the presence of pathological specimens with rotated teeth (Yuan and Yang 2004). Wild mammals, mainly Cervidae, dominated the faunal remains in the early and middle Neolithic sites of this region. The proportion of *Sus* in faunal assemblages began to increase in the Songze



Jiahu 2. Cishan 3. Kuahuqiao 4. Dadiwan 5. Yuezhuang 6. Shuangdun 7. Luotuodun 8. Tianluoshan9. Hemudu
 Beiqian 11. Chengtoushan 12. Wayaogou 13. Jiangzhai 14. Quanhucun 15. Xipo 16. Wuzhuangguoliang 17. Kangjia
 Taosi 19. Wadian 20. Xiawanggang 21. Xinzhai 22. Shenggedaliang 23. Donglongshan 24. Qinglongquan
 Dongjiaqiao 26. Longnan 27. Linagzhu (Bianjiashan, Meirendi, Zhongjiagang) 28. Xinglonggou 29. Zhuzhai
 Baijia 31. Baligang

Figure 1. Map of Neolithic sites referred to in this text.

崧泽 Culture (6000 BP) period and subsequently replaced the Cervidae in the Liangzhu 良渚 Culture period (5500 to 4000 BP). Decrease of deer and increase of *Sus* were also reported at Longnan 龙南 in Jiangsu (Okamura 2000). There were, however, intersite variations in the faunal composition in the Yantze Delta sites (Dong and Yuan 2020), and the high proportion of pigs might be a phenomenon only at urban sites (see the discussion on Liangzhu sites below). Wang et al. (2015) studied the faunal remains in the Songze-Liangzhu period context at Dongjiaqiao 董家桥, Zhejiang, and reported that, although the proportion of *Sus* was about 30% of NISP, relatively young individuals between 6 and 24 months old were dominant. Together with the relatively small size of the *Sus*, they suggested the keeping of pigs at the site.

Matsui et al. (2016) compared the relative proportion of taxa in the faunal remains from Early (7000 to 5000 BP) and

Late (5000 to 4000 BP) Neolithic sites in the Lower Yangtze River Valley and reported the drastic decrease of Cervidae and increase of pigs. The faunal assemblages at Early Neolithic sites of Hemudu 河姆渡 and Tianluoshan 田螺山 are characterized by high proportions of Cervidae. The Late Neolithic Sus remains from three localities of Liangzhu Archaeological Ruins 良渚古城 (LAR), Bianjiashan 卞家山, Meirendi 美人 地, and Zhongjiagang 钟家港 were investigated in detail. The Sus remains occupied more than 90 % of identified mammal remains both at Meirendi and Bianjiashan (Matsui et al. 2016; Kikuchi et al. 2020). The mandibular M3 length measurements of Sus samples range c. 22 to 26 mm at Meirendi and 28.42 to 42.84 mm at Bianjiashan, suggesting that hunting of the wild boar continued, while domestic pigs were kept and consumed at this site. The investigator proposed that the individuals with M3 length over 40-mm might be wild boar (Zhang 2014; Kikuchi

Region	Site	Culture	Age (BP)	Reference
Yellow River	Cishan 磁山	Cishan 磁山	8100-7000	Zhou (1981)
	Yuezhuang 月庄	Houli 后李	7500-7200	Hu et al. (2008)
	Dadiwan 大地湾	pre-Yangshao (Dadiwan 大地湾 Culture)	7900–7200	Barton et al. (2009)
		Yangshao 仰韶	6500-4900	Barton et al. (2009)
	Beiqian 北阡	Dawenkou 大汶口	6100-5500	Wang et al. (2013)
	Xipo 西坡	Yangshao 仰韶	5800-5500	Ekaterina et al. (2005)
	Wuzhuangguoliang 五庄果梁	Yangshao 仰韶	5500-5000	Guan et al. (2008)
	Wadian 瓦店	Longshan 龙山	5000-4000	Chen et al. (2017)
	Taosi 陶寺	Longshan 龙山	4400-3900	Zhang et al. (2007), Chen et al. (2012)
	Kangjia 康家	Longshan 龙山	4300-4000	Ekaterina et al. (2005)
	Xinzhai 新砦	Longshan 龙山	4100-3800	Wu et al. (2007), Zhang et al. (2015)
	Shengedaliang 神圪垯梁	Longshan 龙山	3800-3600	Chen et al. (2018)
Huai and Han River	Jiahu 贾湖	Peiligang 裴李岗	9000-7500	Luo (2012)
	Shuangdun 双墩	Shuangdun 双墩	7300–6500	Guan et al. (2011)
	Qinglongquan 青龙泉	Yangshao 仰韶	5500-5000	Luo (2012)
		Qujialing 屈家岭	5100-4600	Guo et al. (2011), Chen et al. (2015)
		Shijiahe 石家河	4600-4000	Guo et al. (2011), Chen et al. (2015)
	Xiawanggang 下王岗	Yangshao 仰韶	6600-5400	Cucchi et al. (2016)
		Qujialing 屈家岭	5400-4500	Cucchi et al. (2016)
		Longshan 龙山	4600-3900	Cucchi et al. (2016)
Yangtze River	Kuahuqiao 跨湖桥	Kuahuqiao 跨湖桥	8000-7000	Yoneda et al. (2016)
	Luotuodun 骆驼墩	Majiabang 马家浜	7300-5900	Guan et al. (2019)
	Tianluoshan 田螺山	Hemudu 河姆渡	7000-6000	Minagawa et al. (2010)
	Liangzhu 良渚	Liangzhu 良渚	5300-4500	Yoneda et al. (2016)

Table 1. List of Neolithic sites referred to in the text

et al. 2020). The metric data, however, do not separate clearly into large and small size groups at Tianluoshan, or at the three localities of LAR (Kikuchi et al. 2020: Figure 3-3). The age profile of the Sus from three LAR sites, indicated that young adults between 1 and 2 yr of age were most frequent, although both young individuals and adults over 2 years were present (Zhang 2014; Matsui et al. 2016; Song 2019; Kikuchi et al. 2020). Specimens with tooth pathology, such as rotation of teeth, periodontal disease, and frequent linear enamel hypoplasia (90 of 273 molars from Bianjiashan), were found among the Sus assemblages. The zooarcheologists concluded that many of the Sus found at Tianluoshan and LAR sites were at the early stage of domestication under extensive management. Wild pigs were also hunted, and hybridization between domestic and morphologically wild individuals occurred frequently, resulting in the mixture of wild and domestic morphological characteristics among the Sus bones in the assemblage (Zhang 2014; Matsui et al. 2016; Kikuchi et al. 2020). The management of pigs did not seem to intensify in the following Qianshanyang 钱山漾 Culture period (Neolithic-Early Bronze transition). Deer was dominant in the faunal assemblages, suggesting the exploitation of wild resources continued (Kikuchi et al. 2020).

Multiple origins of pig domestication in China have been suggested based on the different pace of morphological changes observed in the Neolithic pigs in northern and southern China (Luo and Zhang 2008; Yuan 2008). Recent accumulation of genomic evidence can also be interpreted to support a multiregional process of domestication (Xiang et al. 2017). We still do not yet have enough data to make a diachronic or intersite comparison of morphological and demographic changes during the critical period between 9000 and 6000 BP, but the evidence at hand suggests more intensive management strategies of pigs at the sites in the Yellow River Valley.

Domestication of Crops and Development of an Agricultural Economy

The different pace of morphological changes in pigs between the north and south discussed above reflects the regional difference in the degree of human control over *Sus* populations. The management strategy of pigs must have been an integrated part of the regional agricultural economy and was related to the aspects of work allocation and resource availability. We will briefly review the domestication of major crops in northern and southern China, since Neolithic plant cultivation and animal husbandry developed in the process of adapting to the different ecosystems of the two regions in the effort to efficiently utilize their resources.

Domestication of Millets in the Yellow River Valley

Both foxtail millet (*Setaria italica*) and broomcorn millet (*Panicum miliaceum*) were domesticated in the Yellow River

Valley in northern China. Archeobotanical evidence suggests that wild millets had been exploited in the final Paleolithic/ initial Neolithic (see the summary by Stevens et al. 2020). Secure archeobotanical evidences of both Panicum and Setaria were associated with the Cishan Culture period (8100 to 7600 BP) at Cishan, Hebei, the site where the beginning of domestication of pigs in 8000 BP was also suggested (see above). Direct C14 dating of carbonized grains suggest that domestic-type millets began to be found by around 7500 BP in the Yellow River Valley sites (Stevens et al. 2020). Early examples of charred Panicum and Setaria grains were reported from Yuezhuang 月庄 (Houli 后李 Culture, 8000 to 7700 BP) in Shandong (Hu 2008; Crawford et al. 2016). Remains of rice were also found from Yuezhuang, although whether of a wild or domestic status was ambiguous (Crawford et al. 2016). Panicum grains were also reported from Xinglonggou 兴隆沟 (Xinglongwa 兴隆洼 Culture, 8000 to 7500 BP) in Inner Mongolia (Zhao 2011).

In general, broomcorn millet (Panicum miliaceum) was dominant among the millet remains at pre-Yangshao period sites and foxtail millet (Setaria italica) was relatively scarce. Carbonized grains of Panicum were rare, and no Setaria grains were found in the pre-Yangshao Dadiwan 大地湾 Culture contexts (7500 to 7200 BP) at Dadiwan in Gansu. Both Panicum and Setaria grains were attested in the Yangshao period contexts of 6500 to 4900 BP at the same site (Liu et al. 2004). At Beigian 北阡, a Dawenkou 大汶口 Culture site (6100 to 5500 BP) in the eastern periphery of Yellow River Valley on the coast of Shandong Peninsula, Panicum was dominant, although Setaria was also found. The latter became increasingly common through time and became a dominant variety of millet during the Yangshao period when millet cultivation became wide spread in northern China (Barton et al. 2009; Lu et al. 2009; Crawford et al. 2016; Jin et al. 2016; Bestel et al. 2018).

Domestication of Rice in the Yangtze River Valley

In the Yangtze River Valley in southern China, a domestic form of rice was reported as early as 8000 to 7000 BP at Kuahuqiao 跨湖桥in Zhejiang, and rice became the main crop of Neolithic plant cultivation. A shift from exploitation of wild food resources to more intensive subsistence strategies including rice production in irrigated fields and reclaimed land, occurred in the Late Neolithic. Millets also began to be cultivated after 6000 BP. Carbonized grains of foxtail millets were attested in the Daxi 大溪 Culture period contexts (5800 BP) at Chengtoushan 城头山 in Hunan in the middle Yangtze River Valley (Nasu et al. 2007; 2012). Chengtoushan is a site surrounded by moats, where both rice and millet were found. Rice was probably cultivated in the small paddy fields as well as in the wetland of flood plain around the site, while millet was cultivated on the dry farmland on the upland terrace area in the site.

Plant Cultivation in the Huai and Han River Valleys

The environment of Huai and Han River Basin between the two major river valleys was suitable for both dry-land farming of millets and paddy-field rice cultivation. Archeobotanical evidence of rice comes earlier than millet. The rice grains found from Phase 1 of Jiahu (c. 9000 to 8500 BP) were identified as an "early cultivated form with some surviving wild rice characteristics" (Zhang & Hung 2013: 50). Evidence of early pig management was also reported from Jiahu (see above) where isotope analyses of pig remains also provide supportive evidence (see below). Barnyard millet (*Echinochloa* sp.), a C4 plant, was found at Jiahu, but was identified as a wild rice-paddy weed (Zhang & Hung 2013). Over 70% of spikelet bases of rice recovered from pre-Yangshao contexts of Baligang 八里岗 (c. 9000 to 8500 BP), Henan, were of a nonshattering domestic form (Deng



Figure 2. Chronology of Neolithic cultures in China.
2015; Zhang & Hung 2013). Both Jiahu and Baligang are located within the northern limit of distribution of wild rice in the Early Holocene (Fuller 2011: Fig. 1). Charred grains of millets (*Panicum*) were recovered from Zhuzhai 朱寨 (Peiligang 裴李岗 Culture) in Henan (Bestel et al. 2018), and Baijia 白家 (Dadiwan Culture) in Shaanxi, that were directly dated to c. 7700 to 7500 BP (Yang et al. 2016). Evidence of mixed farming of rice and millets (both *Panicum* and *Setaria*) was reported from the Yangshao Culture period context at Baligang (Deng 2015).

The evidence from the Huai and Han River basins as well as from Chengtoushan in the Yangtze River Valley suggest that millets began to spread southward from their center of domestication by the beginning of the Yangshao Culture period, and wherever the environment was suitable, dry-land farming was practiced alongside rice cultivation as part of intensification of agricultural production in the Late Neolithic.

Isotope Evidence as an Indicator of the Management of Pigs

Light stable isotope ratios of carbon and nitrogen in bone collagen can be a powerful tool in evaluating the degree of human influence over Sus populations during the early stages of domestication process. That is, when some pigs began to adapt to the anthropogenic niche, human induced selection pressure was not strong enough to cause phenotype changes (Matsui et al. 2005; Minagawa et al. 2005; Price and Hongo 2019). The diet of Sus could also shift by changes in the availability of natural vegetation due to expansion of agricultural fields, or intentional foddering by humans. The bone collagen of wild herbivores feeding exclusively on C3 plants, including deer and wild pigs that were exploited at the Neolithic sites in China, have δ^{13} C values between -25 and -20‰ and δ^{15} N values between 4 and 7‰ (Yoneda et al. 2016, based on the data of wild pigs from Neolithic southern China and Jomon period Japan). The δ^{13} C values in herbivores would change when the animals had C4 plants in their diet. Millets are C4 plants with c. 15% enrichment in the δ^{13} C value compared with C3 plants. Elevated δ^{13} C values in the bone collagen of *Sus*, therefore, have been interpreted as an indicator of human influence in their diet (Hu et al. 2008), for example, raiding a millet field or feeding in the field after harvest, or possibly the foddering of millet leaves or grains. We have to take some cautions, however, because wild C4 plants might be available in some places in northern China.

Since nitrogen isotope values reflect the trophic levels and are related to the protein intake in the animals' diet (Schoeninger & DeNiro 1984; Bocherens & Drucker 2003), the enrichment of nitrogen isotope ratios of *Sus* indicates the shift to a more omnivorous diet. Such a dietary shift could also occur under influence of humans, for example, when wild pigs had opportunities to scavenge settlement waste, or if some young pigs of wild origin were captured and penned for later consumption and provisioned kitchen waste.

The isotope ratio of strontium (⁸⁷Sr/⁸⁶Sr) in the hard tissue of animals is useful in investigating hunting and husbandry practice. Strontium is taken into animals' bodies through food and water, and its isotope ratios reflects the geological characteristics of the animals' habitat (Bentley 2006). Therefore, strontium isotope ratios of *Sus* give us some insight into the procurement or intersite transfer of animals and animal products.

Dietary Analyses of Sus From Neolithic Sites in China, Using Carbon and Nitrogen Isotope Ratios

Yellow River Valley

Carbon and nitrogen isotope data of Sus from Neolithic sites in the Yellow River Valley are plotted in Figure 3. The pre-Yangshao period samples are available from Phase 1 (7900 to 7200 BP) at Dadiwan (Barton et al. 2009: Figure 2B). Although only a few samples were analyzed, the δ^{13} C values concentrate around -20%, and the δ^{15} N values range from 5 to 7‰. These values are similar to those of herbivores that mainly consume C3 plants. Another set of pre-Yangshao isotope data comes from the Houli Culture context (7500 to 7200 BP) at Yuezhuang in the lower Yellow River Valley, where millet and rice grains were attested as early as 8000 BP. One of the Sus samples from Yuezhuang had an enriched δ^{13} C value and another had a high $\delta^{15}N$ value. Some researchers argued for the beginning of cultivation of millet at this site (see above). Management of pigs could also have been initiated earlier in the lower Yellow River Valley than in upstream regions, but the sample size at Yuezhuang was too small to evaluate the possibility.

Also located in the northeast, some *Sus* samples from Beiqian (6100 to 5500 BP), a Dawenkou Culture site located on the coast of Shandong Peninsula, yielded somewhat elevated δ^{13} C values, but the values were lower than those of the *Sus* samples from contemporary sites in the middle Yellow River Valley.

Many of the samples in Phase 2 of Dadiwan (Yangshao Culture period, 6500 to 4900 BP) showed enrichment of both δ^{13} C and δ^{15} N values. This shift in the diet of Sus at Dadiwan took place by around 5800 BP, which was interpreted as evidence for the domestication of pigs beginning sometime between 7200 and 5800 BP. The dietary shift of Sus coincided in timing with the findings of carbonized grains of both foxtail and broomcorn millets at the site (see above). The δ^{13} C values, however, are scattered between -20 and -6%, suggesting that the proportion of C4 plants in the diet of Sus varied widely. The samples with elevated δ^{13} C values also showed a tendency of higher δ^{15} N values, between 7 and 9‰, which were similar to those of dogs, suggesting that the Sus that were given millet leaves or even grains and also had access to settlement waste. The researchers suggested that the small number of individuals with intermediate $\delta 13C$ and $\delta^{15}N$ values represent wild pigs or extensively managed individuals that had only occasional access to C4 plants and kitchen waste (Barton et al. 2009: 5526 and Figure 2B). Isotope data of the Yangshao Culture period were also available from Xipo西坡 in Henan, and Wuzhuangguoliang 五庄果梁 in Shaanxi. The Sus samples of these sites showed enrichment in both δ^{13} C and δ^{15} N values. In contrast to the wide range of variation in δ^{13} C observed



Figure 3. Carbon and nitrogen isotope ratios of Sus samples from Neolithic sites in the Yellow River Valley.

in Dadiwan, pigs from Xipo and Wuzhuangguoliang seemed heavily dependent on C4 plants (Figure 3).

The isotope data of Sus samples from the Late Neolithic Longshan period after 5000 BP in the middle Yellow River Valley were reported from Wadian瓦店 (5000~4000BP) and Xinzhai 新砦 (4100~3800 BP) in Henan, Taosi 陶寺 (4400~3900 BP) in Shanxi, and also Kangjia 康家(4300 to 4000 BP) and Shengedaliang 神圪墶梁 (3800 to 3600 BP) in Shaanxi (Chen et al. 2018). The Wadian samples showed a wide range of δ^{13} C values, but most samples from other sites had values between -10 and -6%, indicating a considerable proportion of C4 plants in their diet. Only a few specimens from Xinzhai and Kangjia showed an intermediate δ^{13} C value of -11%. One of the samples from the earlier phase of Xinzhai indicated a presence of Sus that had a value indicative of a herbivores diet of C3 plants, which might have come from a wild boar. This suggests that the natural vegetation around the site was dominated by C3 plants. Nitrogen isotope ratios are also high in most samples of the Longshan Culture period, but those from Wadian and the later phase of Xinzhai (3900 to 3800 BP) were variable. Thus, C4 plants were generally incorporated in the diet of Sus in the Yangshao Culture period, and by the Longshan Culture period, most of the Sus samples from the Yellow River Valley had high proportions of C4 plants in their diet. There are, however, some sites where carbon and nitrogen isotope ratios were variable, suggesting that each site took a different management strategy in regards to the foddering of pigs. The Longshan Culture period Taosi samples form a group of the highest δ^{13} C values among the Yellow River Valley sites, with values at -6% or higher. The nitrogen isotope ratios were also high (Zhang et al. 2007, Chen et al. 2012, 2017). Taosi is a site surrounded by a moat, and probably functioned as a local political and economic center. The high proportion of Sus remains at Taosi (more than 80% of the 4750 identified fragments) (Zhou 2015), as well as the elevated carbon and nitrogen isotope ratios with a narrow range of variation suggest more intensive and controlled management of pigs than that of contemporary Wadian in the same region. The variable carbon and nitrogen isotope ratios at Wadian suggest that some of the pigs were more extensively managed and had less access to settlement wastes and/or C4 plants. Wadian is a residential site located in the southern border of the millet farming zone, where the contribution of C4 plants in the diet could be more variable than Taosi on the northern bank of the Yellow River. Hunting of wild pigs was uncommon at either site, as none of the Sus

samples had the isotope ratios typical of herbivores feeding on C3 plants.

Yangtze River Valley

Isotope analyses have been carried out at several Neolithic sites in the Yangtze Delta (Figure 4). Carbon and nitrogen isotope ratios of *Sus* samples from Luotuodun 骆驼墩, a Majiabang 马家浜 Culture site (7300 to 5900 BP), were not different from those of herbivores with C3 plant diet (Guan et al. 2019). Only the distribution ranges of the isotope values were available from Kuahuquiao (Peiligang Culture, 8000 to 7000 BP) and Liangzhu **b** (Liangzhu Culture, 5300 to 4500 BP). The earliest evidence of domestic rice and the claim of the management of pigs were reported from Kuahuquiao. Yoneda et al. (2016: Figure 3) compared carbon and nitrogen isotope ratios in the bone collagen of deer, dog, pigs, and humans from Bianjiashan and Meirendi in LAR with those from Kuahuquiao and Tianluoshan (data from Minagawa 2010). The pig samples from all four sites showed

the δ^{13} C values of a C3 plant diet, but nitrogen isotope ratios had a wide range. Some *Sus* samples from Kuahuqiao included specimens with elevated δ^{15} N values around 8 to 10‰, which is comparable to the values of humans and dogs, while others showed no enrichment in the δ^{15} N values. A diverse pig diet was suggested at Tianluoshan and two localities of LAR (Minagawa 2010; Yoneda 2016), with the δ^{15} N values ranging between a ratio similar to that of deer and a ratio close to humans. There is no clear dichotomy among the samples that might be expected if both domestic pigs that were provisioned kitchen waste and wild pigs that fed on natural vegetation were present.

The results of isotope analyses suggest that human influence on the diet of pigs was variable in the Neolithic sites in the Yangtze Delta: while some individuals were either fed by humans or had frequent access to settlement wastes, others were free-ranging and/or subsisted mainly on C3 plants (Minagawa 2010; Yoneda 2016).

These isotopic results on *Sus* from Tianluoshan and the LAR sites corroborate the results of morphological studies at these



●Tianluoshan田螺山 △Luotuodun骆驼墩

Figure 4. Carbon and nitrogen isotope ratios of Sus samples from Neolithic sites in the Yangtze River Valley.

sites, which was that although both wild and domestic pigs were present, the two groups could not be clearly distinguished based on morphological characteristics. Management strategies of pigs in the Yangtze Delta sites tended to be extensive ones, which took advantage of the rich natural vegetation in the region, without regular provisioning of fodder. Strict control over breeding was not practiced either, allowing hybridization between the managed pigs and the wild *Sus* population. Although millet cultivation began as early as 5800 BP in the middle Yangtze Valley (Nasu et al. 2007, 2012, see above), there is no indication of C4 plants in the diet of *Sus* in the Neolithic Yangtze Delta sites.

Huai and Han River Valley

In the region between the two major river valleys, pig management strategies exhibited various trajectories. Analysis of carbon isotopes in pig bones from Jiahu in Henan supports the claim based on morphological study of having the earliest evidence of pig domestication. A sample from Jiahu had elevated nitrogen isotope ratios (Luo 2012), and a few other samples showed the δ^{13} C values of a C4 plant diet (Figure 5). Although domestic millets have not been found at Jiahu, wild C4 plants have been identified (see above). The presence of a few specimens that showed the isotope values of herbivores with C3 diet, however, suggests that C3 plants were dominant in the natural vegetation around the site. Therefore, human influence on the diet of at least some pigs is strongly suggested at Jiahu. Samples from Shuangdun 双墩 (7300 to 6500 BP) also had a wide range of δ^{15} N values, between 4 and 8 ‰. There are also a few samples that had elevated carbon isotope ratios around -12‰, suggesting a mixed C3 and C4 plant diet. During the Yangshao Culture period and later, both carbon and nitrogen isotope values of Sus samples varied widely. Qinglongquan 青龙泉 (5500 to 4000 BP) located near Han River in Hubei, and Xiawanggang下王岗 (6600 to 3900 BP, Cucchi et al. 2016) provide the long sequence of the Yangshao, Qujialing 屈家岭, and Shijiahe 石家河 or Longshan Culture periods. Carbon isotope ratios of Sus from the Yangshao phase at Qinglongquan indicate a diet of mainly C3 plants, but the δ^{13} C values became variable from the following Qujialing period, suggesting that C4 plants were incorporated into the diet of pigs. Increasing variability in the nitrogen isotope ratios, ranging between 4 and 7‰, is also observed starting in the Yangshao contexts. A similar tendency was observed at Xiawanggang. Samples with intermediate δ^{13} C values between C3 and C4 plants had already existed among the Yangshao period Sus remains. Clear separation between the samples indicating C3 and C4 diets was observed only in the Longshan period (Cucchi et al. 2016). The samples with elevated δ^{13} C values tend to also have higher δ^{15} N values at Qinglongquan during the Quijaling and Shijiahe Culture periods, which might suggest the foddering of both kitchen waste and C4 plants (Guo et al. 2011, Chen et al. 2015).

Strontium Isotope Analysis

The enamel of mandibular third molars of the Sus from the three localities of Liangzhu Archaeological Ruins (LAR), Bianjiashan, Meirendi, and Zhongjiagang, were sampled for strontium isotope analysis. The strontium isotope ratios were variable both within and between each locality, ranging from 0.71022 to 0.71290, and the total range of variation at the three LAR sites was 0.00268. The strontium ratio in the immediate vicinity of LAR was 0.713, and closer values to the *Sus* samples were found in the locations about 4 to 10 km from the sites. This result suggests that the *Sus* remains found at LAR sites were supplied from multiple locations to the sites for consumption.

The strontium isotope ratios of *Sus* obtained from the samples from Wadian and Taosi of the middle Yellow River Valley were more consistent, and were not discrepant from the geological values of the sites (Zhao et al. 2011, 2012). The total range of variation found among the samples was 0.00167, much smaller compared with the Yangtze Delta sites. The homogeneous strontium values suggest that the pigs consumed at the two Neolithic sites were locally obtained, and were possibly raised within the sites for local consumption. As discussed above, foddering of millets and kitchen waste to the pigs was suggested by the enrichment in both carbon and nitrogen isotope values of the samples from these two sites. Thus, a more controlled and intensive management of pigs integrated in the economic activities of the settlements was suggested at the Yellow River Valley Neolithic sites compared with that in the Yangtze River Valley sites.

Discussion: Regional Comparison of Pig Management Strategies in Neolithic China

Both morphological and isotopic evidences suggest that the Neolithic sites in the Yellow River Valley and the lower Yangtze delta adopted different strategies of pig management. In the Yellow River Valley sites, pigs were managed more intensively: they were probably penned, and kitchen waste and C4 plants were given as fodder. The contribution of C4 plants became significant from the Yangshao period, when millet cultivation became wide-spread in northern China, suggesting that pigs were either given millet stubble or allowed to feed in the millet field after harvest, if not being given the millet grains. The degree of enrichment of nitrogen isotope ratios varies between sites, but the values are relatively consistent within each site. Therefore, each site probably used a somewhat different combination of fodder according to their economy and the local vegetation. Hunting of wild pigs was rare.

In the Yangtze Delta sites such as Tianluoshan and Liangzhu Archaeological Ruins, pigs were managed more extensively than those in the Yellow River Valley sites. While some pigs had scavenged or were provisioned kitchen waste and perhaps penned, others mainly consumed C3 plants. Hunting of wild pigs continued and hybridization between wild individuals and extensively managed individuals was probably frequent.

The difference in the pig management strategies between the Yellow River Valley and Yangtze River Valley sites probably reflects the environmental differences in the two regions during the transitional period from the Hypsithermal to a drier and colder climate around 5000 BP. The Yellow River Valley sites in the north were more severely affected by the climate change



Figure 5. Carbon and nitrogen isotope ratios of Sus samples from Neolithic sites in the Han and Huai River Valley.

and had to take a more intensive strategy to increase production in both agriculture and animal husbandry to sustain the population. Foddering with C4 plants may have already started at the initial stage of domestication of pigs in the north, which became common practice in pig management. As more land was converted to farming fields in the effort to increase agricultural production, extensive management of pigs probably became impossible.

There is no indication of the foddering of pigs with C4 plants at the southern sites, even after millets were introduced to middle Yangtze River Valley sites such as Chengtoushan. Rice was the major crop, but not necessarily the major food in the tradition of broad-spectrum resource utilization in southern China. A wide range of food resources including nuts, water caltrop, fish, and wild mammals were procured alongside rice production in the Yangtze Delta sites throughout the Neolithic. Millets were added as another food resource where suitable farmland was available. In the middle Yangtze Valley, the effort to increase production took the form of more diversification

of agriculture, while production of rice was intensified by technological innovations such as irrigation to expand the paddy fields. Millets and later wheat were added to the agricultural inventory, and gross agricultural productivity was increased by converting the terraces to farmland. In the course of diversification in agricultural development, pig management also found a suitable niche by efficiently utilizing the abundant natural vegetation as well as settlement waste for fodder, but control over pig population was rather extensive. The proportion of wild mammals in the faunal assemblages probably remained high throughout the Neolithic, as well as the Bronze Age, with the exception of urban sites in the Liangzhu Culture.

This contrasts with the more focused millet production in the Yellow River Valley where higher competition probably existed between animal husbandry and plant cultivation over suitable fields. Thus, pig management in the north took the trajectory of more intensive control over pig population including foddering of millet by-products and strict separation between wild and domestic pig population, possibly by penning of pigs at the sites. The management strategies of pigs were more variable at sites in the Huai and Han River Basin between the two major river valleys. It seems that an extensive management strategy, similar to that in the Yangtze River valley sites, was employed at pre-Yangshao sites, but a small number of pigs at these sites were eating C4 plants. The variation in both δ^{13} C and δ^{15} N values starting from the Yangshao period indicates a versatile strategy probably taken at the household level.

Conclusion

Although we do not have enough data at hand to determine whether the initial process of domestication of pigs in China had either single or multiple origins, zooarcheological evidence suggests that management of pigs began around 9000 to 8000 BP in both north and south China. Different trajectories in the intensification of pig management between the northern and southern regions can be observed in the Middle Neolithic period, beginning around 6500 BP.

Morphological and metric data as well as the isotope data of archeological pig remains suggest a higher degree of control over pigs in northern China. Carbon and nitrogen isotope analyses of bone collagen of archeological *Sus* remains suggest a shift in the diet in northern China from the Yangshao Culture period, when dry-land farming of millets was widespread in the Yellow River Valley. In the north, pigs were likely penned at sites and given kitchen waste and C4 plants as fodder. The further intensification of pig management in the north which occurred during the Longshan Culture period may be placed in the context of overall intensification of food production in northern China in the transitional period from the Hypsithermal to a colder and drier climate, coinciding with the introduction of wheat, cattle, and sheep around 4500 BP (Yuan 2008).

In the Yangtze Delta sites, enrichment of nitrogen isotope ratios in the bone collagen of some of the Sus samples is observed as early as 8000 BP, but the hunting of wild boar seems to have continued, and morphological differences between domestic and wild pigs are not clear-cut. The abundance of natural vegetation in the warmer and wetter environment in southern China and availability of nuts (Quercus sp.) and probably root-crops made more extensive management of pigs possible. The high proportion of pigs at urban sites in the Liangzhu Culture Period suggests that the urban sites depended on pigs supplied to them from surrounding settlements. Hunting of wild boar and deer continued well into the Late Neolithic, and even during the Bronze Age. Although millets were cultivated in the Yangtze River Valley by 6000 BP, there is no indication of the foddering of millets or other C4 plants to the pigs. More intersite variation in pig management practice was observed at sites of the Huai and Han river basin, located between the two major river valleys. The region received influence from both northern and southern Neolithic cultures, and the environment was suitable for both dry-land farming of millets and rice paddy farming. We need, however, more pig isotope data from nonurban sites in the Yangtze River Valley,

especially from the sites where millets were found to confirm the differences in foddering practice from the sites in north China.

Acknowledgments

The authors are grateful to the editors and the two anonymous reviewers for their editorial comments and constructive suggestions. The research was supported by the SOKENDAI Advanced Sciences Synergy Program (SASSP) 2020, JSPS/MEXT Grants-in-Aid for Scientific Research 20H05819, 18H05444 and 18H00754.



Hitomi Hongo is an associate professor at School of Advanced Sciences, The Graduate University for Advanced Studies (SOKENDAI). She received her PhD in anthropology from Harvard University. Her main research interest is the domestication process of ungulates both in Southwest Asia and East Asia. She has worked as an zooarcheologist in excavations of prehistoric sites in Turkey, Syria, Iran, and Jordan. Corresponding author: hongouhm@soken.ac.jp

Hiroki Kikuchi is a postdoctoral research fellow at School of Advanced Sciences, The Graduate University for Advanced Studies (SOKENDAI). He is a specialist in Chinese archeology and zooarcheology. He has about 20 years of research experience in archeological projects in China. Recently, his research interest focuses on the horse culture in ancient East Asia.





Hiroo Nasu received his PhD in archeobotany from the SOKENDAI (The Graduate University for Advanced Studies) of Japan. He has joined the Yangtze River Civilization Project as a graduate student, and he has joined the excavation at the Chengtoushan, middle Yangtze in China. He is currently an associate professor of the Center for

Fundamental Education at the Okayama University of Science, Japan. His research focuses on plant domestication and the origin of agriculture in East Asia and Mesoamerica.

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Feature Article The domestication of South American camelids: a review

Hugo D. Yacobaccio

CONICET-Instituto de Arqueología, Universidad de Buenos Aires, Buenos Aires, Argentina

Implications

- Appearance of individuals larger than the current llama (earliest evidence around 7100 cal. BP, increasing between 5800 and 4200 cal. BP).
- Detection of human impact due to environmental management practices that suggests more intensive human intervention in the environment since ca. 5300–4869 cal. AP.
- Detection of pathologies indicative of human handling in bones of the extremities and vertebrae since ca. 4900 cal. AP.
- First appearance of corrals in caves or in stone structures in deep ravines on the edge of valleys between 4500 and 3639 cal. AP.

Key words: South American camelid, domestication process, Mid-Holocene, Southern Andes

Introduction

South American camelids are the only domesticated ungulates in the Americas, and the Andean region sustained the only pastoralist societies in the pre-Hispanic New World. South American Camelids are composed by two genera and four species, two of them wild (vicuñas *Vicugna vicugna* Molina, 1782, and guanacos *Lama guanicoe* Müller, 1776) and two domestic (llamas *Lama glama* Linnaeus, 1758 and alpacas *Lama pacos* Cuvier, 1800 suggested *Vicugna pacos* Linnaeus, 1758 by Wheeler et al., 2006) (Figure 1).

Guanacos have a broad geographic distribution across a variety of open habitats (arid, semiarid, hilly, mountain, steppe) and temperate forest environments. Their social structure reflects this wide distribution, with some plasticity in types of groups. In the breeding season, the guanaco social structure comprises three basic units: territorial family groups, nonterritorial male groups, and solitary individuals. In turn, mixed groups are common during the winter and in some populations migration occurs. Family group territoriality in the breeding season is correlated with stable food supply (Vilá, 2012: 64). Vicuñas live only in high-altitude Puna environments above 3,400 m in Peru, Bolivia, Argentina, and Chile. They are adapted to open grasslands and steppes; although they prefer to graze in the humid wetlands or marshes (vegas), due to the presence of livestock in these wetlands, vicuñas are usually found in the steppes. Vicuñas live in family groups consisting of one male, three to four females, and two offspring, and in bachelor groups. Family groups are stable and territorial all year round (Vilá, 2012: 42–43).

During pre-Hispanic times, the domestic llamas were circumscribed to the Andean regions of Perú, Bolivia, Chile, and Argentina, but alpacas had a more restricted habitat in the high and humid punas (bofedales) of Perú, Bolivia, and northern Chile.

The domestication of camelids was a complex process associated with the adaptations of hunter-gatherer groups to environmental fragmentation, caused by increased aridity during the Mid-Holocene and the consequent loss of productive habitats in the region (Yacobaccio et al., 2017). During this period, hunter-gatherer groups adopted a logistic strategy, reducing their residential mobility and introducing technological innovations. They developed communal hunts of wild camelids, made possible by population aggregation during their annual cycle, and opted for specialized hunting of camelids as their main source of food (Aschero and Martínez, 2001). Table 1 summarizes the correlated changes in the environment and in human populations by period. These changes did not happen all at once across the region; the geography of the origins of animal domestication and social complexity can be best described as a mosaic pattern.

Domestication is a process of interaction between an animal species and humans. Darwin (1868) made explicit that domestication includes the raising of animals in captivity that can occur without a conscious effort on the part of people and increases animal fertility, allowing them to have greater plasticity. According to Price (1984, 2002), domestication is an evolutionary process marked by the genotypic adaptation of animals to the captive environment. A domesticated

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Guanaco Wild-Salka



(Lama guanicoe)

Two subespecies: Lama guanicoe cacsilensis (north) Lama guanicoe guanicoe (south)

Weight 100-120 kgs. Height at the withers 120 cms.



Vicuña Wild- Salka



(Vicugna vicugna)

Two subespecies: Vicugna vicugna mensalis (north) Vicugna vicugna vicugna (south)

Weight 45 kgs. Height at the withers 90 cms.





(Lama pacos, suggested Vicugna pacos)

Two breeds: Suri (long straight fiber) Huacaya (wavy fiber)

Weight 60 kgs. Height at the withers 90 cms.



Figure 1. The four camelids: taxonomy, subspecies, breeds, and original distribution. Salka and Uywa are the Quechua names for wild and domestic, respectively.

Table 1. Correlation between climate,	environment, and main features	of the archeological record for the human
occupations for the Holocene		

Period	Climate and environment	Features of human occupation
Early Holocene (12890–9200 cal. BP)	Stable, moist, and cold	First human settlement of the region
	Weak seasonality in precipitation	Small occupations
	Positive hidrological balance	Low artifact diversity
		Low transport rates of artifacts between localities
		Opportunistic use of animal resources (high diversity)
		Residential mobility
Middle Holocene I (9200–7100 cal. BP)	Arid and warm, marked seasonality in precipitation	More diversity of projectile points
	Environmental fragmentation	New hunting techniques with new weapon kits
	Negative hydrological balance	Grinding tools
	Shor-term climatic variations	Logistical mobility
	Long-term directional variation toward aridity	Specialization in animal use
Middle Holocene II (7100–3770 cal. BP)	Extreme regional aridity	Subsistence diversification (camelid domestication and introduction of cultivated plants)
	Negative hydrological balance	Social complexity
	Fragmentation with habitat loss	Reduction of mobility
	Short term incremental variation (first ENSO)	Appearance of the first villages at the end of the period
	Slightly more humid as from 4470 cal. BP	

animal is one whose mate selection is influenced by humans and whose docility and tolerance to humans are genetically determined.

The first step of the domestication process is based on the relationship of a phenotypically plastic species habituated to human presence, and occurs before any genotypic change; therefore, it can last a long time. This process, called the Baldwin effect, is an evolutionary transition from a facultative tolerance to humans toward a dependence on them; at this stage, the animal population becomes accustomed to the human presence and a selection mechanism for docility begins to function (Crispo, 2007; Francis, 2015).

For llama domestication, a multilocation model has been developed that includes two phases: herd protection and captivity-selective breeding (Yacobaccio and Vilá, 2016). Herd protection refers to human intervention in guanaco populations, or population subgroups, whose individuals are protected from its nonhuman predators and are facilitated access to feeding areas. A second step is the captivity and selective breeding of certain individuals. In the phase of herd protection, channeled by the Baldwin effect, people are a neutral stimulus. In the second step, when people become a positive stimulus-usually associated with the presence of food or shelter-an associative kind of learning emerges that goes beyond habituation and generates the taming process. Tameness is a condition for reproductive manipulation, as well as for the isolation of individuals in confinement or captivity. This step involves a greater degree of handling and isolation, meaning the existence of a physical barrier between wild population and captive herds. The space constraint increases animal density, resulting in changes in the social structure of the group of camelids and triggering genetic adaptation to captivity (Yacobaccio and Vilá, 2016: 10-11).

Of the four pathways of domestication process, camelids are models for the "prey pathway," which includes medium to large ungulates targeted as prey (Larson and Fuller, 2014). In the transition from game management to herd management, hunter-gatherers changed their hunting strategies to maximize the availability of the prey (Larson and Fuller, 2014). In the Southern Andes, this is suggested by several proxy data. The representation of camelid bone remains in archeofaunal assemblages increased through time from 29.7% to nearly 90%, whereas other taxa, generally small fauna, are markedly reduced (Figure 2).

The composition of zooarcheological assemblages and their temporal change is reflected in their diversity (Shannon H) and dominance (D) indices. The Shannon H index accounts for the abundance and evenness of species in an assemblage, and D is a measure of dominance that reveals the most conspicuous and abundant species. From the Early to the Mid-Holocene II (12890-3770 cal. BP), diversity decreased from 0.93 to 0.29, whereas D increased from 0.52 to 0.84 (Yacobaccio, 2013; Yacobaccio et al., 2017). These two measures can be used as proxies of generalized vs. specialized use of fauna, in this particular case, camelids. The most ancient radiocarbon dates associated to this change in diversity and dominance indices have a pooled mean of 6177 ± 39 cal. BP. This suggests that before that date, hunter-gatherers had a mostly generalized subsistence base on a regional scale in which different habitats were used according to gross species abundance, with the exception of patches that offered a limited range of resources in great quantities, like some rodent colonies or bird nesting places. After ca. 6200 cal. BP, a specialized economic system emerged and resilient habitats were used mainly to increase the use of the focal resource. The emergence of this economic system based on the intensification of the use of camelids coincided



Figure 2. Use of animal resources during the Holocene in the high Andean region of Northwestern Argentina and northern Chile. Box and jitter graph of data represented in percent of identified bones from 28 archeological sites. See location of some of them in Figure 3.

with the earliest evidence for herd protection (Yacobaccio and Vilá, 2016: 9).

Here we will review the evidence for the domestication of camelids in the Southern Andes arranged according to the steps of the model described above. I recommend a recent review of the evidence for the Central Andes by Moore (2016). However, in Discussion and Conclusion, I will compare some specific issues between both regions.

Genetic Evidence

Genetic studies have shown that the two wild species belong to two distinct groups and are therefore good taxonomic genera. Vicuñas are differentiated into two clades; that is, they are two parts of a group that descend from a common ancestor, according to their subspecific assignment (the northern, Vicugna vicugna mensalis and the southern Vicugna vicugna vicugna). Guanacos can also be divided into two subspecies: the northern L. g. cacsilensis and the southern L. g. guanicoe, the latter having a greater distribution that includes the southern Andes and Patagonia (Kadwell et al., 2001; Marin et al., 2017). Llamas and guanacos form a monophyletic group in a clear antecessorderived species process. Alpacas are associated with vicuñas from mitochondrial genome (Marín et al., 2017), and also associated with the guanaco lineage when microsatellites were analyzed (Kadwell et al., 2001). Microsatellites notwithstanding, these studies concluded that the llama was derived from the guanaco and the alpaca from the vicuña (Wheeler et al., 2006; Marin et al., 2017).

An analysis of genetic diversity in the hypervariable region of the mitochondrial genome in Bolivian llamas and alpacas published by Barreta et al. (2013) confirmed that guanacos are

the ancestors of llamas, but the origin of alpacas remains unclear (Barreta et al., 2013). The article found exclusive haplotypes shared between alpacas and vicuñas, but a significant number of alpacas (51%-63% of the samples) were found to belong in the guanaco clade. This indicates a high degree of hybridization, suggesting that alpacas had a mixed origin, or alternatively, that an introgression occurred during or after domestication. If the first hypothesis were confirmed, it would provide strong proof that alpacas were domesticated after the llama. The mitochondrial control region indicates that all the haplotypes shared between guanacos and alpacas also exist in llamas. This could indicate that hybrids between domestic forms were common. The model derived from the results of Barreta et al.'s article lend support to the idea that alpacas resulted from interbreeding between vicuñas and llamas. Likewise, from the confirmation of the existence of two lineages of guanacos (northern and southern) and the finding that some llamas share haplotypes with southern guanacos, they conclude: "The present study would support also at the genetic level and taking into account the archaeological evidence, the existence of additional llama domestication centres in Argentina and Bolivia" (Barreta et al., 2013: 8). The hybridization produced since the 16th century AD, after the Spanish conquest of the Andes, produced mitochondrial lineages shared between different species, limiting the power of this line of inquiry to clarify the origins of domestic camelids. For this reason, it is of fundamental importance to carry out paleogenomic studies. Of the various studies carried out in South American camelids (Weinstock et al., 2009; Westbury et al., 2016; Díaz Marotto, 2018; Abbonna et al., 2020), we will comment here on Díaz Marotto (2018) for its relevance. The author analyzed samples from three archeological sites in the Salar de Atacama area (Chile) dated between 2750 and 2500 cal. BP. This work does not refer to the earliest moments of domestication, but rather to the moment when pastoralism became the predominant economic strategy among local human groups. Díaz Marotto studied the complete genome of 77 bone samples, obtaining conclusive evidence that llamas were domesticated derivates of guanacos. In this case, a distinction between subspecies of guanacos was made, confirming that both L. g. guanicoe and L. g. cacsilensis were the ancestors, in contrast with previous studies of current genomes (Marín et al., 2007) that had proposed L. cacsilensis as the only ancestor. In turn, the complete mitochondrial genome of alpacas shows that this species, also domesticated before the Spanish conquest, has a much closer relationship with the guanaco/llama lineage than with vicuñas. Díaz Marotto determined a clade of domestic species where llamas and alpacas are grouped very closely, suggesting that the llama was the first domesticated species, followed by the emergence of alpacas as a result of sustained interbreeding of female llamas with male vicuñas. Likewise, she agreed with Barreta et al. (2013) that the South-Central Andes was a domestication center independent from that of the Central Andes, based on the evidence of the domestication of the L. g. guanicoe subspecies. This conclusion is in line with more general arguments about the number of

domestication events in ungulates. The use of genetic sequences has led numerous authors to conclude that animal domestication was a great deal more frequent and evenly distributed than previously thought. This claim is based "on the affinity between DNA sequences of domestic animals and their wild counterparts and the assumption that branching patterns on phylogenetic trees reflect independent domestication episodes. This rationale has been used to support claims for multiple and independent domestications of genetically and geographically divergent populations" (Larson and Fuller, 2014: 214). This argument takes into consideration pigs, goats, sheep, horses, cows, and now, we may add, llamas.

Main Archeological Evidence

Osteometry has been used as a proxy to study the domestication process by detecting changes in the size of individuals. Indeed, South American camelids have a size gradient from smallest to largest: vicuña-alpaca-northern guanacollama. This defines two groups: the small one-vicuñas and alpacas-and the large one-guanacos and llamas. As can be seen, both groups contain wild and domestic camelids. In the large group, there is a complicated fact, and it is the variability of the guanaco size; L. guanicoe has a high clinal dispersion, which influences its size. Patagonian or southern guanacos are much larger than northern or North Andean ones. That is why we have to be very careful with the reference measurements used to compare with archeological samples. These issues have been widely debated in Andean zooarcheology (Izeta, 2008; Cartajena, 2009; Gasco et al., 2014; Hernández and L'Heureux, 2019). In the large group, the variation in guanaco size imposes certain restrictions on the determination of species (guanaco vs. llama) based on osteometry alone. There is a "zone of uncertainty" defined by an overlap in size between small llamas and North Andean guanacos. However, the larger measurements beyond this overlap zone can be determined as L. glama without a doubt.

As far as we know today, the first osteological evidence of a change in size in camelids that could reveal the modifications produced by a domestication process made its first appearance in the Southern Andes at approximately 7100 yr cal. BP. This evidence is an increase in the width of the distal metacarpus, along with an increase in the size and robustness of other bones, such as phalanges, scapulae, and humerus. These specimens are larger than the known sizes for North Andean guanacos, and are comparable to modern llamas, or even larger (Cartajena et al., 2007). This points to the emergence of a camelid similar in size to the largest among current llamas. In the herd protection phase (7100-4500 cal. BP), there was an increase in size variability, especially with the emergence of very large specimens that were first detected in the archeological record at the Hornillos 2 site (layer 2), but later increased their distribution significantly between 5800 and 4200 cal. AP, when their presence was noted in numerous archeological sites in the region (Izeta, 2010, Figure 3).

The variation in size that we refer to here is summarized in Figure 4. From the variation in breadth of the phalanx I facies articularis proximalis, it can be inferred that between 4900 and 4700 cal. BP, there was a significant proportion of camelids that were larger than current llamas, followed by a reduction in size by 2600 cal. BP, setting the median and interquartile range equal to that of current llamas. From that date on, bone remains equivalent to the size of current llamas were found in other ecosystems, such as mesothermal valleys (between 1500 and 2900 masl) and the lowlands of the Chaco, in numerous archeological sites (Izeta, 2010, Mercolli, 2019, Del Papa, 2020). At 580 cal. BP, during the Inka period, the size of llamas completely coincides with that of today.

Harbers et al. (2020) found that "mobility reduction induces a plastic response beyond the shape variation of wild boars in their natural habitat, associated with a reduction in the range of locomotor behaviours and muscle loads" and that produces changes in the calcaneus shape due to captivity. This is extremely interesting because identifies osteological modification as a consequence of confinement. The case of llamas seems to have been different because there was no such a reduction in mobility on that scale. Moreover, as llamas were used as pack animals, their mobility remained to be high. However, the zooarcheological record shows a reduction of size variability after pens appeared as can be seen in Figure 4, where size become stabilized since 2600 cal. BP. Recent research on morphometric analysis made on guanaco and llamas first phalanges are promising, but no conclusive vet because the two species have not been differentiated in these analyses (Hernández and L'Hereux, 2019).

Other paleoenvironmental and archeological evidence accompanied the change in size of the camelids and point toward a change in the camelid-human relationship. Pollen analysis in several localities of the Puna has identified a greater abundance of Chenopodiaceae–Amaranthaceae and *Pennisetum* from ca. 5300 to 4869 cal. BP, which is consistent with more intensive human impact on wetlands due to environmental management practices, perhaps including periodic burning to increase patch productivity.

This change in the human-camelid relationship is also seen in the appearance of bone pathologies. Cartajena et al. (2007) recorded periostitis in distal phalanges and metapodia from the Tulán 52 (ca. 4900 cal. BP), and Puripica 1 (ca. 4700 cal. BP) sites. These exostoses are due to the proliferation of the bone, possibly caused by long-term irritation of the periosteum. They also observed osteophytes produced by arthropathies due to the living conditions of the animals, perhaps related to the long periods of exercise that are characteristic of pack animals. Labarca Encina and Gallardo (2015) analyzed 14 bones with pathologies from the Topater 1 cemetery (Calama, Chile) dated between 2517 and 1868 cal. BP. Most of the pathologies occur in limb bones that, due to their size, have been assigned to L. glama. At this site, most of the phalanges show exostoses, an abnormal formation of new tissue on the outside of the bone. Its manifestation is mild to moderate and is located in the diaphysis and, to a lesser extent, on the dorsal and lateral faces



Figure 3. Map showing selected sites with camelid domestication evidence. 1. Hornillos 2; 2. Alero Cuevas; 3. Tulán 52; 4. Puripica 1; 5. Inca Cueva 7; 6. Pozo Cavado; 7. Alero Sin Cabeza; 8. Huachichocana III; 9. Alero Unquillar; 10. Tulán 54; 11. Cueva Quispe; 12. Casa Chávez Montículos; 13. Huirunpure; 14. Topater 1.

of the epiphyses. These pathologies were attributed to constant trauma to the joints and could result from environmental factors, such as walking on uneven ground, as well as the excessive use of the animal due to cultural practices, as would be the case of pack animals. A llama head with articulated vertebrae recovered from an inhumation at the Huachichocana III site (3170 and 2867 cal. BP, Figure 3) also provided information on bone pathology. The cervical vertebra C2 (axis) presents periostitis due to direct trauma caused by a tie rope or due to an excessive use of this articular section of the neck. The use of a muzzle to restrain the animal is the most probable explanation for this pathology. In addition, the analysis of stable carbon and nitrogen isotopes reinforces the idea that this specimen's diet was strongly determined by human intervention (Yacobaccio et al., 2018).

The use of muzzles at such an early time would not be uncommon, as ropes had already begun to appear in the archeological record. These ropes can be interpreted as a technological innovation related to the onset of pastoralism. Indeed, at Alero Unquillar (Figure 3), in which two metapodia were determined to belong to a llama by osteometry, a rope made with local grasses dated at 3989–3570 cal. BP was recovered. Likewise, the grave goods of human burial number 4 in the Huachichocana III site included remains of ropes made with palm leaf fibers and local bromeliads (*Tillandsia usneoides* or *Deuterocohnia*; Lema, 2017). This burial is relatively contemporary with burial 3—the one containing the llama head—and it could be associated with two radiocarbon dates from ca. 3360 to 3170 cal. BP. The appearance of ropes has direct implications for the development of gripping or restraining technology associated with herd management.

A change in phase of the domestication process occurred with the emergence of confinement technology, that is, pens. The first corrals were small caves, such as Inca Cave 7, whose entrance was covered by a wall of stone boulders. Given its size, it was probably used to keep young camelids in confinement. A layer of guano that covered the ground within the cave was helped to determine its function as a corral (Figure 5). As mentioned above, two metapodia determined as belonging to very large llamas were recovered from this site. The corralling episode has been dated between 4635 and 4232 cal. BP. In the Tulán gorge, Cartajena et al. (2007: 168) observed that the "high and rocky slopes are used as natural boundaries on both borders; on softer slopes big regular boulders have been arranged to enclose pens. Boundary lines that cross the ravine are interrupted in the stream part to avoid holding back



Figure 4. Measurement of the breadth of the phalanx I facies articularis proximalis (Bfp) through time. Between 4900 and 4700 cal. BP, larger animals than today llamas are noted. Later, the sizes are the same as the current llamas and bigger than northern guanacos.

the water; palisades or similar solutions were probably used to bound areas close to the stream, allowing the enclosure of pens.[...] Pen dimensions (ca. 300×80 m) suggest a considerable amount of labour." This corral can be dated at around 2600 cal. BP.

Discussion and Conclusion

The transition from hunting to herding has been a complex one. Herd protection involved changes in camelid behavior, but also modifications in the human strategies used to approach wild camelids. This phase lasted for a long time, from 7100 to 4500 cal. BP, when corrals made their first appearance in the region.

Environmental fragmentation promoted the aggregation of humans and wildlife in resilient habitats, such as wetlands, thus creating the conditions for the development of a closer and more stable relationship between people and camelids. Then, as a condition for herd protecting and habituation, human communities reduced their mobility, stabilizing their residence in these areas where grazing resources were more concentrated. The entire time span characterized by herd protection also was accompanied by an increase in human population. The archeological sites show evidence of more intensive occupation at this time, and about 4900 cal. BP, the first site with several stone enclosures could have functioned as places where human populations gathered periodically (Núñez and Perlès, 2018).

Moreover, the grouping of radiocarbon dates from archeological sites in the region has been analyzed as indicators of human demography or anthropogenic signal in the Holocene (Muscio and López, 2016). This study suggests that after 6177 cal. BP, the anthropogenic signal increased, reaching its maximum at 4700 cal. BP. This date correlates quite well with the



Figure 5. Layer of feces (guano) on the ground of Inca Cueva 7, dated in 4635 and 4232 cal. BP. This is the most ancient evidence of pens from Northwestern Argentina.

appearance of corrals or courtyards in the archeological record, which points toward an intensification of the camelid domestication process. This is a significant finding because, for the diffusion of an innovation to take place—in this case, domesticated animals—there need to be long-reaching interaction networks sustained by large, interconnected populations. Evidence of such interaction networks can be provided by the existence of domestic llamas in the microthermal valleys and lowlands of the Chaco region since at least 2100 cal. BP, which reveals a relatively rapid dispersion of this innovation.

This process is contemporary with what happened in the Central Andes, in which early domestication indicators in the Puna de Junín occurred between 5470 and 3480 cal. BP (Moore, 2016). In southern Peru, in the Osmore Valley, evidence of domestication appeared between 4090 and 3677 cal. BP (Aldenderfer, 1998).

Taking the Andes as a whole, the knowledge that we have about the domestication of camelids is still very fragmentary, since there are portions of territory with no archeological evidence on the period that concerns us. Likewise, more genetic studies on ancient materials are needed, although according to what we know today, llamas would have been domesticated first and later, alpacas, which resulted from introgressions of llamas with vicuñas (Barreta et al., 2013; Díaz Marotto, 2018).

There are still many unresolved issues and unanswered questions concerning the domestication of South American camelids. The next few years will hold many new and exciting insights for researchers in this challenging field.

Acknowledgments

I acknowledge Paloma Fernández Díaz Marotto for allowing me to comment on her data. I also thank Bibiana Vilá for her revision on the manuscript, and her useful suggestions, and

About the Authors



Hugo Yacobaccio has obtained PhD from the University of Buenos Aires. Currently, he is superior researcher of the National Council of Investigation (CONICET), full professor of Archaeological Theory at the University of Buenos Aires, and member of the doctoral teaching com-

mittee at the University of Tucuman. His fields of interest are related to environmental archeology, archeozoology, animal domestication, ethnoarcheology, and the peopling of the South Andean Altiplano. Recently, he has been working on climatic change and its effects on pre-Hispanic society of the southern High Andes and on frames of reference for studying climatic change in the past. He also has been involved in projects concerning vicuña use and conservation and, signing several agreements with aboriginal communities of the Altiplano, in order to sistematize, protect, and create an interpretation center for the rock art (now under construction) in Barrancas (Puna of Jujuy Province, Argentina). **Corresponding author:** hdyacobaccio@gmail.com Malena Pirola for revising the English spelling. I am also grateful for the comments of the two anonymous reviewers. As usual, all the mistakes are of my own responsibility. I am also grateful to the editors of this volume, Thomas Cucchi and Benjamin Arbuckle, for their kind invitation to contribute to this article.

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Feature Article

Origin of the domestic chicken from modern biological and zooarchaeological approaches

Masaki Eda

Hokkaido University Museum, Hokkaido University, Kita 10, Nishi 8, Kita-ku, Sapporo Hokkaido 060-0810, Japan

Implications

- Chickens (*Gallus gallus domesticus* or *Gallus domesticus*) are the most common domestic animals worldwide. However, the origin of their domestication is obscure.
- The early 21st century mitochondrial DNA data suggest that various red junglefowl (*Gallus gallus*) subspecies are the wild ancestors of the domestic chicken. However, more recent genomic data reveals that *Gallus gallus spadiceus*, indigenous to northern Thailand, Myanmar, and southwestern China, is its main wild ancestor.
- Domestic chicken bones are detected at early and middle Holocene archaeological sites. However, their authenticity remains controversial, with direct radiocarbon dating and reliable species identification being required.
- The first red junglefowl domestication might have occurred within the native range of the species, especially in the distribution area of *G. g. spadiceus*. Because archaeological red junglefowl may have been present during the various domestication stages, it is believed that its bone analyses will clarify their historical role and relationship with humans in the region.

Key words: chicken, DNA analysis, domestication, medullary bone, red junglefowl, zooarchaeology

Introduction

Chickens (Gallus gallus domesticus or Gallus domesticus) are the most common domestic animals worldwide. In 2017, the global chicken population was >22 billion (FAO, 2020; http://www.fao.org/ poultry-production-products/production/poultry-species/

doi: 10.1093/af/vfab016

chickens/en/). They are bred on all continents and countries except Antarctica and Vatican City (Lawler, 2015). To meet the growing demand for animal foods, high-yielding commercial chicken breeds were developed in recent decades for meat and egg production. Nearly 1,600 different local chicken breeds are internationally recognized (FAO, 2020).

Despite their global distribution, the origin of chicken domestication remains obscure. Two approaches have been used to investigate this subject. First, their morphological, ecological, and genetic characteristics were compared with those of other species using modern biological techniques. Second, the characteristics of the chickens were reconstructed for each era and region using zooarchaeological remains. Herein, prior research on the origin of global chicken domestication using modern biological and zooarchaeological approaches were reviewed, and future perspectives for studies on the origin of domestic chicken were discussed.

Modern Biological Approach: What is the Wild Ancestor of Domestic Chicken?

Single-species vs. multispecies origin of domestic chicken

Charles Darwin proposed that *Gallus bankiva* (current *Gallus gallus*, red junglefowl; Figure 1) was the ancestor of domestic chickens based on several lines of evidence: 1) the extremely close resemblance between red junglefowl and the game fowl (the most typical domestic fowl) regarding color, general structure, and voice; 2) their fertility, when the red junglefowl and game fowl were crossed; 3) the possibility of the wild red junglefowl being tamed; and 4) the broad phenotypic variation of the wild red junglefowl (Darwin, 1868). Moreover, Darwin rejected the possibility that the other three *Gallus* wild junglefowl (Ceylon junglefowl (*Gallus lafayetii*), gray junglefowl (*Gallus sonneratii*), and green junglefowl (*Gallus varius*)) could be the primitive stocks of the domestic chicken as hybrids derived from these species crossed with the domestic chicken were usually infertile.

Darwin assertions about the origins of domestic chickens were widely accepted and certain researchers considered the matter settled (e.g., Beebe, 1921). Nevertheless, others suggested a polyphyletic origin of domestic chicken, including two possibilities: 1) all are descendants of two or more of the four extant wild junglefowl species or 2) Mediterranean breeds, such as white leghorns, may in fact

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Figure 1. Wild red junglefowl in Kuala Lumpur, Malaysia. Photograph taken by the author.

be red junglefowl descendants, whereas Asiatic breeds, such as Cochins, Brahmas, and Langshans, may have originated from some other extinct ancestors (Hutt, 1949). The second scenario could be explained by the difference between existing junglefowl (as well as Mediterranean breeds) and Asiatic breeds regarding their morphophysiological traits and temperament. Apart from the possibilities that certain extinct ancestors may have given rise to Asiatic breeds, the polyphyletic origin of domestic chicken was indicated by phenotypic characteristics that could have derived from other wild junglefowl (e.g., extended black plumage may have originated from green junglefowl and yellow skin may have originated from gray junglefowl) and given the fact that hybrids of any *Gallus* wild junglefowl and domestic chicken were in some cases fertile (Hutt, 1949).

Evidences of single-species origin of domestic chicken

Molecular analyses revealed a close genetic relationship between domestic chicken and red junglefowl, which harbor very similar egg proteins (Baker, 1968). In contrast, their G_2 globulin was distinct from that of gray junglefowl. Hence, red junglefowl might be the main progenitor of domestic chicken (Baker, 1968). The close relatedness between the domestic chicken and red junglefowl was further demonstrated by phylogenetic analyses of the domestic chicken and four *Gallus* junglefowl via blood protein and DNA fingerprinting. Moreover, analyses of the 400 base-pair (bp) nucleotide sequence of the mitochondrial DNA (mtDNA) control region in four wild junglefowl species and nine domestic chicken breeds revealed a monophyletic relationship between domestic chicken and red junglefowl (Fumihito et al., 1996).

Single-subspecies versus multisubspecies origin of domestic chicken

There are five extant red junglefowl subspecies: Gallus gallus gallus, Gallus gallus spadiceus, Gallus gallus jabouillei, Gallus



Figure 2. Map of the geographic distribution of the wild junglefowl according to Wang et al. (2020).

gallus murghi, and Gallus gallus bankiva (Figure 2). However, there are morphological intergradations among the four continental subspecies. Fumihito et al. (1996) reported that *G. g. bankiva* was distinct from *G. g. spadiceus* and *G. g. gallus*. They also showed that the nine domestic chicken breeds and the continental *G. g. gallus* population in Southeast Asia formed a single cluster in the phylogenetic tree. Hence, that population might be the sole ancestor of all domestic chicken breeds, originating from a single domestication event in Thailand and adjacent regions (Fumihito et al., 1996).

Nonetheless, Liu et al. (2006) indicated that Fumihito et al. (1996) lacked the analysis of domestic chicken breeds and wild red junglefowl subspecies from China and India and comprised small sample sizes. To overcome these constraints, Liu et al. (2006) analyzed the partial mtDNA control regions of 834 domestic chickens across Eurasia and of 66 red junglefowl, including four subspecies but not G. g. murghi. The phylogenetic analysis revealed two main clades of which were formed by G. g. bankiva sequences and by sequences of other continental subspecies and domestic chickens (Liu et al., 2006) (Figure 3). The latter consisted of nine highly divergent mtDNA clades (A-I). Gallus g. spadiceus and G. g. jabouillei were observed mainly in clades A, B, and F, whereas G. g. gallus was observed mainly in clades D, H, and I. Clades A-G and I included domestic chickens. Clades A, B, and E were ubiquitously distributed among Eurasian chickens, whereas the others were mainly confined to South and Southeast Asian chickens. Clades F and G were mostly restricted to Yunnan, whereas clade C was distributed over southern and southeastern China and Japan. Based on these distinct distribution patterns and population expansion signature of each clade, Liu et al. (2006) suggested that various clades may have originated from different regions and multiple independent domestication events might have occurred. The multiple domestication event hypothesis was supported by additional sampling of G. g. murghi and domestic chickens from India, with extensive mtDNA control region analysis of 4,732 domestic chickens and 206 red junglefowl and 61 mtDNA genome studies of representative haplotypes (Miao et al., 2013).



Figure 3. Unrooted neighbor-joining tree of 169 haplotypes from 834 domestic chickens and 66 red junglefowl obtained by Liu et al. (2006).

Evidences of multispecies origin of domestic chicken

Nonetheless, genetic analysis of the yellow skin pigmentation, which is common to numerous commercial chicken breeds, revealed that the red junglefowl was not the sole wild ancestor of the domestic chicken (Eriksson et al., 2008). Domestic chickens with yellow skin are homozygous for a recessive allele, whereas white-skinned chickens bear one or more dominant allele. Eriksson et al. (2008) showed that the recessive allele associated with yellow skin was caused by regulatory mutation(s) in the dermal β -carotene dioxygenase 2 (*BCDO2*). Phylogenetic analysis of chickens and four wild junglefowl based on a 23.8-kb sequence comprising the BCDO2 locus showed that white-skinned breeds clustered with red junglefowl, whereas yellow-skinned breeds clustered with gray and green junglefowl. Thus, the vellow skin allele might have originated from a different species, most likely gray junglefowl (Eriksson et al., 2008).

The polyphyletic species origin of domestic chicken was corroborated by recent genome-wide studies. Lawal et al. (2020) analyzed the genomes of 53 indigenous village chickens, nine red junglefowl, as well as three other junglefowl species and the common pheasant (*Phasianus colchicus*). The data suggested that the red junglefowl was the main ancestral species of domestic chickens and their divergence of domestic chickens and red junglefowl may have occurred 8,093 years ago (range: 7,014–8,768 years). There was also extensive bidirectional introgression between the gray junglefowl and domestic chickens, a few introgression signatures between domestic chickens and Ceylon junglefowl, and a single introgression signature between domestic chickens and green junglefowl (Lawal et al., 2020).

Wang et al. (2020) analyzed 863 genomes from worldwide sampling of chickens, representatives of all four *Gallus* junglefowl species and of all five red junglefowl subspecies. In the phylogenetic tree, all domestic chickens formed a monophyletic clade with *G. g. spadiceus* (Figure 4). In

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addition, a principal component analysis disclosed relatively closer genetic affinity between the domestic chicken and G. g. spadiceus, suggesting that the subspecies was their closest progenitor. A molecular clock analysis further indicated that the domestic chicken diverged from G. g. spadiceus $9,500 \pm 3,300$ years ago, although this point does not necessarily correlate with the beginning of the domestication process. Once again, there was evidence of admixture between other junglefowl species and domestic chickens. However, the introgression fragments occurred at a very low frequency and were confined mainly to local chickens inhabiting the native ranges of all local wild junglefowl, except gray junglefowl (Wang et al., 2020). The authors concluded that the domestic chickens were initially derived from G. g. spadiceus in southwestern China, northern Thailand, and Myanmar, translocated across Southeast and South Asia, and interbred with other local red junglefowl subspecies and junglefowl species (Wang et al., 2020). Wang et al. (2020) also indicated that previous studies using mtDNA analysis were unable to confirm the origins of domestic chickens owing to recurrent hybridizations shared mtDNA from wild relatives and domestic chickens.

Summary

Based on its morphological, physiological, and behavioral traits, red junglefowl was considered the main ancestor of domestic chicken in the late 19th century (Darwin, 1868), which was supported by molecular data collected in the 20th century (Baker, 1968; Fumihito et al., 1996). However, the mtDNA analyses from the early 21st century suggested multiple *G. gallus* subspecies as the wild ancestors of the domestic chicken (Liu et al., 2006; Miao et al., 2013). Moreover, recent genome data revealed that the red junglefowl subspecies *G. g. spadiceus* is the main wild ancestor, which was translocated across Southeast and South Asia and locally interbred with other red junglefowl subspecies (Wang et al., 2020).



Figure 4. Maximum-likelihood phylogenetic tree showing the monophyletic clade formed by domestic chickens with *Gallus gallus spadiceus* as the nearest wild progenitor. Black dots at nodes indicate \geq 99% bootstrap support. Domestic chicken and red junglefowl clades are collapsed and colored according to geographic range and subspecies classification (Wang et al., 2020).

This hypothesis explains the origin of certain morphological features, such as yellow skin, derived from the gray junglefowl and currently present in domestic chickens but absent in red junglefowls (Eriksson et al., 2008).

Zooarchaeological Approach: Where can the Oldest Domestic Chicken Bones be Found?

Candidate sites for the oldest domestic chicken bone

Frederick Zeuner suggested that chickens were first domesticated in the Indus Valley region ca. 2000 BC (Zeuner, 1963) based on seals and figurines depicting chicken and a chicken femur found at Mohenjo-Daro, Pakistan (Sewell and Guha, 1931). In 1988, West and Zhou (1988) reviewed archaeological sites with chicken bones from before the 1st century AD. They listed 90 archaeological sites containing chicken bones in Europe, the Middle East, South Asia, and East Asia. They introduced Cishan (Hebei Province; 5405 ± 100 to 5285 ± 105 BC), Peiligang (Henan Province; 5935 ± 480 to 5495 ± 200 BC) (Figure 5), and 16 other Neolithic Chinese sites predating Mohenjo-Daro and concluded that chickens were first domesticated in Southeast Asia, transported north, and established in China (West and Zhou, 1988).

Phasianidae bones from Cishan were identified as domesticated chickens for three reasons (Zhou, 1981). First, Cishan is located far north of the natural distribution range of wild red junglefowl, which is restricted to southern China. Second, tarsometatarsi with spurs were more abundant at that site than tarsometatarsi without spurs. As, in general, male birds have spurs but females do not, Zhou (1981) discussed a possible male-biased chicken butchering and regarded it as proof of domestication. Third, spurred tarsometatarsi from Cishan (range: 72.0–86.5 mm; mean: 79.0 mm) were, on average, longer than those of modern male wild red junglefowl (range: 70.0–82.0 mm; mean: 78.7 mm). According to West and Zhou (1988), northern China can be one of the early centers of chicken domestication (with some caution) given that the numerous putative chicken bones have been recorded at several archaeological sites (Serjeantson, 2009).

Xiang et al. (2014) published an intriguing article on early Holocene domestic chicken in northern China. Phasianidae bones from Nanzhuangtou (n = 22; Hebei Province; 10000– 7600 BC), Cishan (n = 7), Wangyin (n = 6; Shandong Province; 4500–3500 BC), and Jiuliandun (n = 4; Hebei Province; 500– 200 BC) were subjected to ancient DNA analysis. Species identification using a 159-bp fragment of the mtDNA cytochrome c oxidase subunit I gene revealed that each of the 13 sequences obtained (seven from Nanzhuangtou, one from Cishan, three from Wangyin, and two from Jiuliandun) were identified as *Gallus* since they were closer to *Gallus* than to any other genus, such as *Phasianus*, *Alectoris*, *Lophura*, *Tetraophasis*, and *Syrmaticus*.

Xiang et al. (2014) also succeeded in the analysis of a 326-bp fragment of the mtDNA control region in eight samples (three from Nanzhuangtou, one from Cishan, two from Wangyin, and two from Jiuliandun). The median-joining network constructed



Figure 5. Previously reported archaeological sites of chicken bones. Sites with (circles) and without (triangles) chicken bones from the Neolithic (gray) and Bronze Age (white) in China (after Eda et al., 2016) are indicated. Sites reported by Eda et al. (2016) (star; 1. Nanzhuangtou; 2. Cishan; 3. Wangyin; 4. Zaoshugounao; 5. Xiawanggang) are also shown. Of note, candidate chicken bones were found only in Zaoshugounao and Xiawanggang.

based on the obtained sequences, 10 published ancient chicken sequences, and 1,001 extant published sequences from four *Gallus* species showed that all samples were included in three of the five main haplogroups of modern domestic chickens. Thus, the bones originated from domestic chicken. As there were abundant remains of tropical animal and plant species excavated at Cishan and Nanzhuangtou, Xiang et al. (2014) estimated that the North China Plain was warmer and more humid with much larger forest cover and was a suitable habitat for junglefowl during the early Holocene. They concluded that the distribution range of the wild red junglefowl was far wider in the early Holocene than in the present and that domestic chicken farming began ~10,000 years ago in northern China (Xiang et al., 2014).

Challenges to the early and middle Holocene chicken domestication in northern China

The report by Xiang et al. on domestic chickens in northern China during the early and middle Holocene was questioned in two subsequent papers. Peng et al. (2015) criticized the improper incorporation of the primer in the analyzed DNA sequence and the insufficiency of the analyzed sequence length. Xiang et al. (2015b) admitted the mistake, but they insisted that the main conclusion was unchanged by these limitations. In turn, Peters et al. (2015) also raised several questions: improper incorporation of the primer sequence, unsuitability of the climatic condition of northern China for red junglefowl, difficulty of ancient DNA sequence amplification based on the thermal age calculation, suspicion on the morphological identification of the analyzed samples, and possibility of contamination from the later cultural deposits. Xiang et al. (2015a) contradicted these questions and concluded "further discussions confirm early Holocene chicken domestication in northern China" in the title of their reply letter.

Several studies challenged the hypothesis that early and middle Holocene chicken domestication and Neolithic poultry husbandry occurred in northern China. Pitt et al. (2016) estimated the suitability of the modern and mid-Holocene (ca. 4000 BC) of this region for red junglefowl distribution and found that the climate of northern China did not meet these requirements during either period. Furthermore, Huang et al. (2018) analyzed the modern domestic chicken mtDNA with a focus on certain haplogroups that were absent in red junglefowl samples and were restricted to domestic chickens. They disclosed a recent domestic chicken expansion in northern China from a maternal perspective and denied early Holocene chicken domestication in this region. Following their review of Holocene paleoclimate and archaeofaunal archives, Peters et al. (2016) concluded that the habitat requirements of (sub-)tropical red junglefowl were absent during the early and middle Holocene of northern China. They also suggested that the middle Yangtze River basin delimited the northernmost boundary of a thermally optimal habitat for red junglefowl during the Holocene.

Eda et al. (2016) analyzed 280 Phasianidae hindlimb bones (femur, tibiotarsus, and tarsometatarsus) from 11 Neolithic sites, including Nanzhuangtou (n = 7), Cishan (n = 5), and Wangyin (n = 70), and eight Bronze Age sites in China (Figure 5), based on the morphological identification criteria. Because their approach was focused on the discrimination of chickens and red junglefowl from indigenous Japanese pheasants, they were unable to distinguish chickens and red junglefowl from the other 62 indigenous Phasianidae species in China. Nevertheless, the criteria used were useful to exclude nonchicken and nonred junglefowl bones, identifying candidate chicken or red junglefowl bones (Eda et al., 2016). Only one potential chicken bone was identified from the Neolithic period (at Xiawanggang) and only two potential chicken bones were identified from the early Bronze Age (at Zaoshugounao). The other Phasianidae bones, including those from Nanzhuangtou, Cishan, and Wangyin, were identified as nonchicken bones. Therefore, these findings suggest that chickens were not widely kept and red junglefowl were not extensively distributed throughout central and northern China during the early and middle Holocene.

Hence, their results radically differed from those reported for Neolithic and Bronze age domestic chicken exploitation by Xiang et al. (2014), Zhou (1981), and others. For the archaeological Phasianidae remains at Nanzhuangtou, Cishan, and Wangyin, Xiang et al. (2014) identified by ancient DNA analysis 11 bones belonging to chicken or Gallus junglefowl. In contrast, Eda et al. (2016) morphologically classified all 81 bones as nonchicken. These studies markedly differ in terms of the presence or absence of chicken and other Phasianidae bones. Xiang et al. (2014) analyzed at least two canid bones (Peters et al., 2015), more specifically the right canid metacarpi (Eda et al., 2016), and demonstrated them as "typical ancient chicken bones unearthed in northern China" (Xiang et al., 2014). Although Xiang et al. (2015a) insisted that they did not succeed in identifying the species of the canid bones and their identity has no bearing on the conclusions drawn by Xiang et al. (2014), Eda et al. (2016) stated that these bones should be considered "typical" and indicative of the reliability of the samples used by Xiang et al. (2014).

Eda et al. (2016) studied five tarsometatarsi from Cishan, which were probably identified by Zhou (1981) as domestic chicken. All bones had a medial plantar crest absent from the bones of chicken and red junglefowl and were identified as "nonchicken" bones (Eda et al., 2016). Zhou (1981) mentioned that the "oldest domestic chicken in the world" was from Cishan. However, he only stated that the specimens resembled wild red junglefowl in shape and did not explain the criteria for distinguishing chicken bones from those of indigenous birds from northern China. Moreover, Zhou (1981) displayed photographs of four tarsometatarsi with medial plantar crests (Plate 9.1–9.4) and designated them domestic chicken bones. However, no chickens or red junglefowl have a medial planter crest and these bones were obviously misidentified (Eda et al., 2016). The misidentification of tarsometatarsus is more critical than that of other bone elements because Zhou (1981) proposed chicken domestication at Cishan based on measurements and male-biased sex ratios in tarsometatarsus. Therefore, chicken domestication at Cishan is unsubstantiated (Eda et al., 2016). Although chicken bones have been discovered in at least 52 archaeological layers from 44 Neolithic sites and 18 layers from 12 Bronze Age sites in China, these records should be comprehensively reexamined (Eda et al., 2016).

Early Holocene domestic chicken bones in Europe

Pleistocene and early Holocene G. gallus bones were also reported in Europe. Boev (1995) reviewed the Pleistocene and early Holocene archaeological Gallus bones from Moldova, Ukraine, Russia, Crimea, Georgia, Armenia, and Romania and proposed that a glacial refuge may have occurred in the southern Ukraine and Transcaucasus regions, allowing the domestication of the palaeolithic fowl there. In contrast, Mlíkovský (2002) stated that Gallus wild fowl could have been absent in Europe during the Würm III glaciation (ca. 70,000-10,000 years ago) and the middle Holocene. Gallus gallus and other bones dating from the late Pleistocene and early Holocene were found in France, England, Germany, Croatia, Ukraine, Romania, and Greece, with no reliable records in the assigned strata and/or species identification (Mlíkovský, 2002). Domestic chicken bones from the early and middle Holocene have also been reported at certain archaeological sites in Bulgaria. The oldest record was from Hotnista (ca. 5000 BC), in which identified bones were large (~3 kg) and originated from domesticated animals (Boev, 2009). However, Pitt et al. (2016) showed that modern and middle Holocene environmental conditions in Bulgaria were (and are) suboptimal for red junglefowl. Kyselý (2010) argued that these early findings were modest and incoherent and the unusually early dates reported for the European sites should be verified (Kyselý, 2010).

Summary

Thus far, domestic chicken bones have been reported from the early Holocene, for example Nanzhuangtou (northern China, ca. 10,000 years ago; Xiang et al., 2014), Cishan (northern China, ca. 8,000 years ago; Zhou, 1981), and Hotnista (Bulgaria, ca. 7,000 years ago; Boev, 2009) and in several middle Holocene sites in northern China and Europe (reviewed in West and Zhou, 1988; Boev, 1995; Mlíkovský, 2002; Kyselý, 2010). However, the authenticity of these discoveries remains controversial (e.g., Kyselý, 2010; Eda et al., 2016; Peters et al., 2016).

Future Perspectives for Studies of Origin of Domestic Chicken

Reevaluation of the existence of domestic chicken at Mohenjo-Daro

The existence of domestic chicken in Indus Valley ca. 2000 B.C. was taken to be an established fact after Zeuner's (1963) report. Nevertheless, none of the bones was identified as G. g. domesticus or G. domesticus in the original description of Mohenjo-Daro. Instead, they were designated "?Gallus sp." (Sewell and Guha, 1931). The authors defined no criteria to distinguish domestic chicken bones from those of local indigenous Phasianidae species. Hence, it may be said that the identification of "domestic chicken" was unacceptable for the contemporaneous standard. Even if the bones were derived from domestic chickens, it should be verified that they originated from ca. 2000 BC. A femur from Mohenjo-Daro measured 103 mm (Sewell and Guha, 1931), which was larger than those of wild male red junglefowl (~0.7-1.5 kg; range, 74.72–80.04 mm; mean, 76.54 mm; n = 13) and captive male red junglefowl (range, 69.82-80.74 mm; mean, 73.91 mm; n = 24) (Eda, 2020) but similar to those of male Leghorn and Plymouth Rock (both ~3.4 kg).

It is difficult to regard the seals and figurines of chickenlike creatures as solid evidence for the existence of domestic chicken in the Harappan culture. Similarly, it is difficult to consider artistic representations of turtles, monkeys, and rhinoceros in Mohenjo-Daro as evidence of their domestication. Therefore, these discoveries merely suggest that the people during that period recognized similar creatures and the relationships among them. The environmental conditions of Mohenjo-Daro were speculated to be outside of the requirements of red junglefowl during the middle and late Holocene (Pitt et al., 2016). To confirm the existence of domestic chicken at certain early and middle Holocene archaeological sites, radiocarbon dating and accurate species identification of each bone sample are required.

Phasianidae bone research in Southeast Asia

According to environmental considerations, red junglefowl domestication might have occurred within the native range of the species (Pitt et al., 2016). The latest molecular findings pointed to candidate sites in the distribution ranges of *G. g. spadiceus* in western Thailand, the Malaysian Peninsula, and eastern Myanmar, with the time of divergence between domestic chicken and *G. g. spadiceus* being estimated as $9,500 \pm 3,300$ years ago (Wang et al., 2020). The divergence estimate does not determine the origins of domestication but a split between the lineages leading to *spadiceus* and the ancestors of domestic chickens, which, at this point, were likely wild birds. The oldest chicken bones were thought to be intermixed with red junglefowl bones from the Holocene archaeological sites in Southeast Asia. However, reports of bird remains in Southeast Asia are scarce and prehistoric chicken and red junglefowl exploitation is obscure (Storey et al., 2012; Eda et al., 2019). Bone dating and species identification are essential to identify the oldest chickens in the world.

In regards to bone dating, the majority of the zooarchaeological specimens were dated using stratigraphic and/or contextual evidence. However, chicken bones can easily move between occupation phases; hence, precautions are required if samples were from sites with overlaying building structures or archaeological strata (Flink et al. 2014). For example, Flink et al. (2014) directly dated a chicken bone found from Iron Age La Tène C/D contexts (280–15 BC) and revealed the bone was actually from the early modern or modern period (1800 \pm 30 AD). To confirm the age, direct radiocarbon dating of specimens are ideal, although it requires some destruction of the samples.

In regards to species identification, 43 Phasianidae fowl/ pheasant species inhabit Southeast Asia. As far as I know, no morphological criteria have been established to distinguish chicken and red junglefowl from other indigenous fowl/ pheasant bones. Ancient DNA analysis was used to effectively identify archaeological Phasianidae bones (Storey et al., 2012; Xiang et al., 2014; Prendergast et al., 2017; Barton et al., 2020). For the archaeological sites in Southeast Asia, Storey et al. (2012) analyzed the mitochondrial DNA control region of 10 "chicken" (including a stork coracoid; Eda et al., 2019) samples from Ban Non Wat (central Thailand, 3750-1500 BP) and produced two reliable and reproductible G. gallus sequences. The low success rate of the analysis could be due to the humid and warm temperature in Southeast Asia. Prendergast et al. (2017) analyzed morphologically identified chicken or Phasianidae bones from eight eastern African archaeological sites using ancient DNA analysis. They only succeeded to identify 6 (including five chicken and one hornbill) of 28 bones by polymerase chain reaction-based analysis. Then, they reanalyzed 19 of the specimens, which the previous analysis approach failed to identify, using high-throughput (shotgun) sequencing combined with BLAST-based computational analysis, and succeeded to identify six samples (including two Gallus and four indigenous pheasants) at the genus level (Prendergast et al., 2017). The high-throughput sequencing approach would be also useful for the Phasianidae bone identification in Southeast Asia. Moreover, Eda et al. (2020) found collagen peptide peaks, which were useful for discriminating domestic chicken and red junglefowl from indigenous Japanese pheasants, and successfully identified archaeological Phasianidae bones from a Japanese archaeological site. Some of the advantages of using bone collagen over DNA for analyzing archaeological samples include a higher success rate, need of a smaller amount of sample, and lower cost (Buckley et al., 2010). To date, certain collagen peptide peaks have been identified as being unique to domestic chickens and red junglefowls (Eda et al., 2020), which could also be useful to identify those zooarchaeological bones from Southeast Asia.

Beyond the dichotomy of domestic chicken or wild red junglefowl

It is a major challenge to determine if archaeological red junglefowl bones from Southeast Asia were of wild or domestic origin. For example, although Storey et al. (2012) found G. gallus sequences from Thai archaeological deposits dating approximately 2500 BP and 1550 BP, the data were insufficient to say that the bones were from domestic chicken, given there were no differences between mtDNA sequences of wild and domestic red junglefowl, in particular at the earliest stage of the domestication process (Figure 6). Red junglefowl excavated from various archaeological sites and different periods were not all necessarily at the same stage of domestication. Pure wild junglefowl used to be hunted. If people fed junglefowl, similar to what is suggested in northern China for common pheasants (Barton et al., 2020), the stable isotope ratios of nitrogen and carbon in red junglefowl bones could be different from wild individuals. This distinction might have occurred long before humans began breeding chickens as these animals were already using the resources near human settlements and crop fields.

Even if certain birds were isolated from the wild population via enclosure and/or long-distance transport, successful breeding was nonetheless required to maintain the population. In Phasianidae and most other birds, the medullary bone, a secondary bony structure, forms in medullary cavity in females at ~1 month before and after laying (Simkiss, 1961). Therefore, the appearance of the medullary bone suggests the presence of multiple mature individuals at that location during the breeding season. A high frequency of medullary bone suggests that the environment at the site was conducive to laying. Moreover, the breeding cycle could not start if humans consumed all the eggs laid by the chickens and it might have taken some time before an environment suitable to hatching was established. Chick mortality is in general high; thus, it would be expected for immature bird bones to be detected among the archaeological sites of a society that had prepared an appropriate environment for hatching. Overall, chicken breeding technology might have been introduced in areas where medullary bone and immature bones appeared simultaneously. In the Neolithic and Bronze Age sites of northern China, "candidate chicken" bones were found in sets with Phasianidae bones, including medullary bone and immature Phasianidae bones (Eda et al., 2016).

When the next generation of a breeding population was born, environmentally plastic phenotypic traits, such as bone size and proportions, may have differed from those of the wild population. Modern captive offspring of red junglefowl were generally smaller than wild red junglefowl, but the distal part of the tibiotarsus was thicker and parts of the wing bone were thinner in the former than in the latter (Eda, 2020). Similar morphological differences may have occurred between ancient wild and captive red junglefowl in the earliest stages of domestication (Eda, 2020). Geometric morphometrics would be useful to explore whether such morphological changes occurred in the early stage of domestication.

As domestication progresses further, artificial selection of individuals that lay more eggs, grow larger, and have a particular color of skin and feather could be envisioned.



Figure 6. Plausible relationship history between humans and red junglefowl at various domestication stages.

However, artificial selection would, at the same time, accelerate the rate of genetic drift by decreasing the effective number of individuals attending to breeding. Considering the genetic processes with the greatest potential impact on domestication, changes resulting from artificial selection are directional, whereas genetic drift produces random changes in gene frequencies (Price, 1984). Thus, selection and genetic drift may cause gene variants to disappear completely, thereby reducing genetic variation but also increasing the frequency of initially rare alleles. If a certain gene frequency within a domestic population is changed compared with the wild population, ancient DNA analysis can find whether the population could be domesticated in the original distribution area of the red junglefowl. In contrast, the introduction of wild individuals decelerates both adaptation to artificial environments and the rate of genetic drift.

Genetically determined traits are expected to differ from those of wild populations later in the domestication process. Flink et al. (2014) studied BCDO2 and a putative domestication gene (thyroid-stimulating hormone receptor, TSHR), thought to be linked to photoperiod and reproduction mechanisms, from 80 European ancient chicken bones dated ~280 BC to the 18th century AD. They suggested that the commonality of yellow skin in Western breeds and the near fixation of a missense mutation within TSHR sequence in all modern chickens took place just past 500 years ago. With additional ancient DNA data and Bayesian statistical framework, Loog et al. (2017) showed that strong selection on variant TSHR allele began around 1,100 years ago, coincident with archaeological evidence for intensified chicken production and documented changes in egg and chicken consumption. Intriguingly, Wang et al. (2020) reported that the variant TSHR allele was found at high frequency in G. g. spadiceus (94.0%), whereas it had a frequency of only 5.4% in other red junglefowl subspecies. Further analysis of ancient genomes from chicken and red junglefowl spanning a wide timeframe and geographic areas are required to explain this pattern. Moreover, genome-wide studies of domestic chickens and red junglefowl have revealed some genes bearing selection associated with color phenotype, as well as the regulation of growth, metabolism, and reproduction, and the development of the nervous system, muscle, and bone (Huang et al. 2020, Wang et al. 2020). The selection on these traits also could be revealed by the extensive ancient DNA analysis of chicken bones using high-throughput sequencing technology.

Conclusion

The origin of domestic chicken has been investigated mainly by modern biological and zooarchaeological approaches. The modern biological approach revealed that a red junglefowl subspecies is the main wild ancestor of the domestic chicken. However, other red junglefowl subspecies and wild junglefowl species also contributed to the modern domestic chicken genetic profile. In contrast, zooarchaeological methodology failed to detect archaeological bones that could be reliably identified

About the Author



Masaki Eda studied archeology at the University of Tsukuba and ecology and molecular biology at the Graduate School of Agricultural and Life Sciences, University of Tokyo. After working as a JSPS Research Fellow at Kyushu University, he taught human anatomy at Tottori University as an assistant professor. He has worked at Hokkaido University Museum since 2012. Incorporating the viewpoints and approaches of each field, he mainly

studies archaeological bird bones. He specializes in archaeozoology to elucidate the paleoecology of birds and zooarchaeology to reconstruct human lives with the knowledge they provide. **Corresponding author:** edamsk@museum.hokudai.ac.jp

as those derived from the "oldest domestic chicken". Further zooarchaeological studies on the early and middle Holocene Phasianidae bones of Southeast Asia are required to make this determination. Analysis of archaeological red junglefowl bones from different perspectives should clarify the roles of these animals and their relationships with humans in each region and time period. Domestic chickens have recently been bred to provide meat and eggs worldwide (FAO, 2020). However, their principle ancestor, red junglefowl, weighs <1 kg and lays only four to eight eggs per year (Lawler, 2015). Elucidation of the origin of chicken domestication may provide useful insights into why red junglefowl rather than other bird taxa are the most common poultry and among the most commonly domesticated animals worldwide.

Acknowledgments

I would like to thank Dr. Benjamin S. Arbuckle and Dr. Thomas Cucchi for inviting me for the project. Insightful comments from two anonymous reviewers clarified the strengths and weaknesses of this study. This study was supported by Japan Society for the Promotion of Science KAKENHI (Grant Numbers: JP18H04172 and JP20H01367).

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Feature Article

Why were New World rabbits not domesticated?

Andrew D. Somerville[†] and Nawa Sugiyama[‡]

[†]Department of World Languages and Cultures, Iowa State University, Ames, IA, USA [‡]Department of Anthropology, University of California, Riverside, CA, USA

Implications

- A greater diversity of rabbit species occurs in North America compared with Europe.
- Archeological evidence demonstrates thousands of years of human-rabbit interactions in both Europe and North America, particularly at the ancient city of Teotihuacan (~AD 1–550) in central Mexico where several studies suggest practices of rabbit management by humans.
- The European rabbit (*Oryctolagus cuniculus*) is the only lagomorph species to have been domesticated by humans.
- This review finds that behavioral differences between European and North American rabbits explain their differential suitability for domestication.

Key words: domestication, human–animal interactions, lagomorphs, rabbit behavior, Teotihuacan

Introduction

Recent archeological and biological research has produced evidence for thousands of years of interactions between human and leporid (rabbits and hares) populations in both Europe and North America (Canada, United States, and Mexico). Resulting from these relationships, European rabbits (*Oryctolagus cuniculus*) were domesticated in southern France within the last 1500 yr (Carneiro et al., 2011; Irving-Pease et al., 2018), and are now commonly bred around the world for their roles as pets, food, a source of fur, and as laboratory subject animals. North American rabbits, however, were not domesticated in the same manner as their Old World counterpart.

This article explores the factors that may explain this disparity in domestication. We begin by providing a brief evolutionary history of rabbits and hares (family Leporidae).

doi: 10.1093/af/vfab026

We then review the archeological evidence for humanrabbit interactions in both the Old and New Worlds, with an emphasis on new data from the ancient Mexican city of Teotihuacan, where archeological and chemical evidence suggests the importance of rabbits in the local diet and economy. Finally, we consider the biological and behavioral characteristics of European rabbits and North American cottontails, emphasizing traits that probably influenced their differential domestication outcomes.

Leporidae

Together with the pika family (Ochotonidae), the Leporidae belong to the order Lagomorpha. The evolution of the leporid family is complex, but the earliest fossils have been found in eastern Asia during the Early to Middle Eocene epoch (~60 to 40 mya) (Ruedas et al., 2018). Leporids spread to North America and throughout the rest of the Old World and experienced a major radiation during the Miocene epoch (~23 to 5 mya) (Lopez-Martinez, 2008; Flynn et al., 2014). This expansion and diversification was likely due to the worldwide spread of C4 grasslands during this global period of cooling and drying (Ge et al., 2013).

Today, the Leporidae family contains 11 genera and 63 species and occupies all major landmasses on earth (Ruedas et al., 2018). Hares belong to a single genus (Lepus) with 32 individual species that are native to North America, Europe, Africa, and Asia. The colloquial term of "rabbits" includes 10 distinct genera and 31 species (Smith et al., 2018: 87). Although several hare species are native to Europe, the only extant rabbit species is the European rabbit (O. cuniculus). This species includes two subspecies: O. cuniculus algirus and O. cuniculus cuniculus (Ferrand and Branco, 2007; Lopez-Martinez, 2008). The natural range of O. c. algirus is southern and western portion of the Iberian Peninsula, including Spain and Portugal, whereas the range of O. c. cuniculus includes the northeast portion of Spain and southern France (Ferrand and Branco, 2007). These populations probably represent centers of refugia during the Last Glacial Maximum. Genetic and protein analyses indicate that the more northern O. c. cuniculus subspecies was the population from which domesticated rabbits originated (Branco et al., 2000; Ferrand and Branco, 2007; Carneiro et al., 2011). Indeed, all domesticated rabbit breeds including the English lop, the Angora rabbit, and the New Zealand white rabbit, which is the most commonly used species in biomedical research, are all descendants of this northern Iberian population.

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A greater diversity of rabbit species exists in the Americas than in Europe, and they occur in a broader range of environments. Containing 17 species, the most diverse rabbit genus of the New World is *Sylvilagus* (Smith et al., 2018). The most widespread member of the *Sylvilagus* genus and the most common rabbit of North America is the eastern cottontail (*Sylvilagus floridanus*). It occurs from Canada to Venezuela. The two other genera of New World rabbits are the monotypic pygmy rabbits (*Brachylagus idahoensis*), which are found in the western United States, and the monotypic volcano rabbits (*Romerolagus diazi*), which are found in central Mexico.

Human–Rabbit Interactions in Europe

Archeological and textual evidence demonstrate a long history of human-rabbit interaction in Europe (King and Thompson, 1994; Saña, 2013), particularly in the Iberian Peninsula, which is the native range of *Oryctolagus cuniculus* (Lopez-Martinez, 2008). The first interactions between humans and leporids in Europe began in Spain during the Late Pleistocene epoch (~50 to 30 kya) when Neandertals and Anatomically Modern Humans both hunted rabbits for food and fur (Fa et al., 2013). During the terminal Pleistocene and early Holocene in the Iberian peninsula (i.e., Epipaleolithic, Mesolithic, and Neolithic eras; ~11,500 to 4500 BC), rabbits appear to have been among the most commonly hunted and consumed animals by modern humans, with some faunal assemblages containing over 90% rabbit bones (Saña, 2013).

Throughout the middle and late Holocene, rabbits remained an important prey source for humans across the Iberian Peninsula. Roman sources from around the third century BC document the importation of rabbits to the Italian peninsula and describe the raising of rabbits in managed fields and pens for food and hunting (Flux, 1994). Archeological evidence from the Roman and pre-Roman sites of Ambrussum, Lattara, and Pech Mahoin southern France indicates the presence of rabbit bones, and multivariate analyses of skeletal measurements demonstrate they exhibited a larger size than wild populations, suggesting intentional breeding by humans (Watson, 2019a,b; Watson and Gardeisen, 2019). Additionally, a rabbit bone was recovered from the first to second century AD Fishbourne Roman Palace in Britain (Sykes et al., 2019), suggesting management or at least long-distance trade of rabbits at this time.

Human translocation of breeding populations intensified during the Middle Ages, extending the distribution of European rabbits throughout Europe and beyond after around AD 800 (Flux, 1994; Callou, 2003; Irving-Pease et al., 2018). Archeological sites across large portions of Europe frequently contain associated ruins of large rabbit warrens or pillow mounds (Williamson, 2006; Pelletier et al., 2016), demonstrating human management and the importance of leporids in human subsistence. Clear morphological changes associated with human-directed breeding, however, only occurred during the 18th century AD when rabbit pet-keeping became common (Callou, 2003). Today, rabbits represent one of the most widely dispersed and numerous mammalian domesticates across the globe.

Following Zeder (2015: 3191), we define domestication as "a sustained multigenerational, mutualistic relationship in which one organism assumes a significant degree of influence over the reproduction and care of another organism in order to secure a more predictable supply of a resource of interest...." The timing of when O. cuniculus crossed the wild-domesticated boundary is difficult to ascertain, as it was a long-term process rather than a singular historical event (Irving-Pease et al., 2018). Evidence of a strong bottleneck in genetic diversity suggests that a singular population in southern France was domesticated sometime within the last 1500 yr (Carneiro et al., 2011), but morphological changes to the skeleton that distinguish wild from domesticated varieties only appear in the 18th century AD (Callou, 2003). We agree with Larson and Fuller (2014: 127) that the European rabbit (O. cuniculus) likely followed the "directed pathway" to domestication, a process that implies the deliberate attempt by humans to domesticate the animal (Zeder, 2012).

Human–Rabbit Interactions in North America

In North America, rabbits exhibit greater geographic distribution and species diversity than in Europe (Chapman and Litvaitis, 2003). Zooarcheological findings in dry caves of central Mexico containing cottontail rabbits (Sylvilagus sp.) indicate their use for food and fur since at least the terminal Pleistocene (Flannery, 1967). After the domestication of plants and the development of farming communities, rabbits remained important sources of food for societies across Canada, the United States, and Mexico. For instance, Lapham et al.'s summary of zooarcheological remains from seven sites in Oaxaca, Mexico, spanning from archaic hunter gatherers campsites (Guila Naguitz, 8700 to 8000 BC) to Early Postclassic cities (Mitla and El Palmillo, AD 1100) demonstrated a consistent pattern of rabbit usage similar to, or even more prevalent than the domesticated dog or turkey (Lapham et al., 2013: Table 3). They argue that rabbits were significant contributors to animal economies at several of the sites they examined, especially at the site of El Palmillo where not only did they contribute between 28% and 39% of the number of identified specimens, they were utilized as food, within rituals, and for their fur, an important component of textile production. Later, in Hernan Cortez's letters to King George, he described the sale of rabbits at the Aztec marketplace of Tlateloco during the early 16th century AD (Cortés, 1977: 110-114). The best archeological evidence of intensive human-leporid interactions at a single settlement comes from the central Mexican metropolis of Teotihuacan.

Leporids of Teotihuacan

The ancient city of Teotihuacan, Mexico (AD 1–550) provides one of the best case studies to understand intensive human–leporid interactions in an urban landscape. The

city extended over 20 km² and housed a population of about 100,000 inhabitants in orthogonal apartment compounds (Cowgill, 2015). Leporids constituted 23% of the minimum number of individuals (MNI) of the Classic Teotihuacan fauna remains analyzed (Sugiyama et al., 2017: Table 3). This total is double the MNI percentage attributed to deer, one of Mesoamerica's premier large herbivores that was utilized as a standard protein source in other pre-Hispanic urban centers (e.g., Maya sites) (Pohl, 1991; Sharpe et al., 2018; Sugiyama et al., 2018, 2020). In comparison to lagomorph indices (ratio of hares to rabbits) in the southwestern United States, where a large proportion of hares compared to rabbits suggests that large communal hare drives helped sustain human populations (Potter, 1997, 2000), Lepus/Sylvilagus ratios at Teotihuacan (0.47) indicate the greater prevalence of rabbits over hares (Sugiyama et al., 2017). One possible explanation is that hares were acquired opportunistically through garden hunting (Linares, 1976), whereas rabbits were not only hunted in the gardens but also captured and opportunistically or extensively kept in the homes. It is particularly noteworthy that a spatial analysis of rabbit and hare remains resulted in a greater density of leporids in the city's core compared with the periphery, with a particular emphasis on rabbits over hares in various areas along the ceremonial core (Sugiyama, et al., 2017).

The best evidence for rabbit captivity and breeding within the city of Teotihuacan was found within a residential apartment complex in the northeast of the city (N6W3) called Oztoyahualco (Manzanilla, 1993). The archaeological, zooarcheological, and isotopic data suggest household level captive breeding of rabbits not only provided a reliable source of proteins, lipids, and fur to their residents, but was also specialized economic task that generated a surplus to be sold/traded. Archeological indicators of rabbit captivity included several smaller room blocks with high phosphate levels in the floors indicative of the area where the rabbits may have been penned or butchered. Additionally, a stone sculpture of a rabbit found in the central plaza suggests this animal was symbolically and/or economically important to the residents. The zooarcheological report of the compound indicated one of the largest concentrations of leporids from a single context, accounting for 46% of the total faunal assemblage, many of which were obtained from the fill of the aforementioned room blocks with high phosphate levels (Valadez Azúa, 1993). Stable carbon isotope analysis indicates that leporids from Oztoyahualco consumed significantly greater amounts of C4 or CAM plants, such as maize or cactus, than did leporids from other sectors of the city, a pattern that suggests human provisioning of the animals, either in managed fields or within the compound itself (Somerville et al., 2016, 2017). Notably, a diverse mix of leporids was present at Oztoyahualco, including three genera (Lepus, Romerolagus, and Sylvilagus) and six species (R. diazi, S. audubonii, S. floridanus, S. cunicularius, L. callotis, and L. californicus), with the eastern cottontail (S. floridanus) being the most commonly represented (Valadez Azúa, 1993: Table 17).

Together, the archeological and isotopic data suggest that humans were provisioning leporids at the Oztoyahualco compound of Teotihuacan and likely producing them for food, fur, and ritual. This emphasis on leporid production and consumption contrasts with the low prevalence of the two domesticated species of Mesoamerica, the dog (*Canis familaris*, 11% MNI) and the turkey (*Meleagris gallopavo*, 6% MNI) (Valadez Azúa, 2003; Manin et al., 2018). Both played a minimal role in dietary practices at Teotihuacan. The presented evidence of rabbits as a predictable source of protein and fat that could be managed at the level of the household or apartment complex.

Evidence of rabbits offered as food for sacrificed animals buried within the Moon and Sun Pyramids at Teotihuacan suggests that rabbits were utilized in state functions. Isotope data confirm that the rabbits found in the stomach contents of ritually sacrificed carnivores, including pumas and eagles, were also fed a diet high in C4 resources. In this way, rabbit production would provide a stable meat source to raise captive carnivores within the city (Sugiyama, et al., 2015). The high concentration of rabbits near the ceremonial core also suggests these predictable resources would have been optimal for use in public feasts and other state functions.

Comparative Sociality

Despite a far greater diversity of leporid species, over 10 millennia of human-rabbit interactions, and centuries of an intensive relationship at Teotihuacan, cottontail rabbits were not domesticated in North America as they were in Europe. Although European rabbits may have followed the directed pathway to domestication, North American rabbits likely embarked on the commensal or prey pathways, but never reached the final destination. Scholars have long noted that the social behavior of an animal is an important factor in the domestication process (Hale, 1969; Price, 1984; Diamond, 1997; Zeder, 2012). In a summary of the behavioral characteristics favorable for domestication, Zeder (2012: 231) identifies four primary areas that render an animal "preadapted" for domestication. These include 1) the social structure of the organism, with favorable traits including large group size, a social hierarchy, and the presence of males within the group; 2) the sexual behavior of the organism, with favorable characteristics including a promiscuous mating system, males being dominant, and the signaling of sexual receptivity by females; 3) parent-young interactions, with favorable characteristics including social imprinting, females accepting young soon after birth, and precocial offspring; 4) the nature of the response to humans, with favorable characteristics including a short flight distance. low reactivity, and the ability to be readily habituated; and 5) the feeding behavior and habitat choice of the organism, with favorable characteristics including a generalist feeding strategy, a wide environmental tolerance, and nonshelter seeking. Here we briefly summarize the behavioral ecology of the European rabbit (O. cuniculus) and that of the eastern cottontail (S. floridanus), which is the most common rabbit of the Americas and was the most abundant species present at Teotihuacan. Because dietary practices,

digestive strategies, habitat preference, and response to humans are similar for these species, we focus the discussion on the first three of these behavioral characteristics that "preadapt" an animal for domestication.

Oryctolagus cuniculus

The natural range of the European rabbit extends across the Iberian Peninsula and varies from woodland to open field habitat. It readily becomes accustomed to human presence and frequently inhabits areas near human settlements. The European rabbit is the only leporid species to form stable social groups under wild conditions (Cowan and Bell, 1986). Groups inhabit multi-entrance burrow and chamber systems known as warrens (Pelletier et al., 2016), which are mostly dug by adult females and can reach up to 3 m in depth (Figure 1). Groups are comprised of a dominant male residing and reproducing with one to multiple females and their young offspring (Lockley, 1975). The population of the warren may range from two to 20 adults. In larger communities, subordinate males and juveniles are also present. O. cuniculus can be considered a gregarious species. In laboratory settings, rabbits raised in individual cages are generally more stressed, less healthy, and display more pathlogical behaviors, including fur pulling and bar biting, than do groupraised rabbits (DiVincenti and Rehrig, 2016).

The mating system of the European rabbit is primarily polygamous, but the exact social arrangement varies from monogamous pairs, to promiscuity, to harem polygyny (Cowan and Bell, 1986). These differences are ultimately influenced by the spatial availability of suitable burrow space, which determines the distribution of females across the landscape and hence the distribution and intersexual competitive dynamics of males (Myers and Poole, 1959; Mykytowycz, 1959). A ridged dominance hierarchy exists separately for each sex; males compete over access to females, whereas females compete over access to suitable territory for burrow space (Cowan and Bell, 1986).

Females give birth to altricial young and nurse infants only for a few minutes once every 24 hr, and weaning is completed within 3 to 4 wk (Bautista et al., 2008; González-Mariscal et al., 2016). Little parental care exists among *O. cuniculus*, but in an experimental setting, males are known to defend juveniles from antagonistic adult does (Mykytowycz and Dudziński, 1972).

Sylvilagus floridanus

The eastern cottontail is the most common and widely distributed rabbit species of the Americas, stretching from southern Canada to Venezuela (Smith et al., 2018). They



Figure 1. Illustration of the (a) European rabbit and its burrow and (b) the eastern cottontail and its burrow. Illustrations by Nathan Thrailkill.

inhabit a variety of ecoregions across their range, but prefer disturbed habitats, such as old fields, shrublands, and generally patchy landscapes with open spaces (Chapman and Litvaitis, 2003; Smith et al., 2018).

The mating system of S. floridanus ranges from promiscuous to polygynous. A ridged and linear dominance hierarchy exists among males, principally resulting from male-male competition over access to receptive females with dominant males obtaining more successful copulations (Marsden and Holler, 1964). The establishment of a defended core territory is not a common practice of S. floridanus; instead, males chase or dislodge lower ranking males when receptive females are present (Brenner and Flemming, 1979; Smith et al., 2018). Although a separate hierarchy exists among females, it is more flexible and less rigidly enforced, which is likely due to the low overall rate of encounters between females (Chapman and Litvaitis, 2003). Male home ranges are larger than female home ranges as they travel greater distances in search of receptive females and because females restrict their ranges in order to stay near their nests to nurse and defend their young (Trent and Rongstad, 1974). Although daily ranges of male and female individuals often overlap, they do not form into stable social groups (Marsden and Holler, 1964). Males and females are primarily solitary with the exception of the interactions between mothers and offspring, which are themselves infrequent.

Eastern cottontail nests are created by females digging shallow and slanted burrows (~10 to 15 cm deep; Figure 1), which they insulate and conceal with fur and grass (Casteel, 1966; Bruch and Chapman, 1983). The females do not enter the burrows, but crouch above them so the young can nurse from below (Nowak and Walker, 1999). Eastern cottontails are also known to create aboveground shelters within protective brush or use existing burrows created by other species. Contact between mothers and infants is minimal, as the mothers visit the young to nurse only for a few minutes once or twice every 24 hr (Verts et al., 1997).

Discussion

Although the European rabbit and the eastern cottontail are similar in many ways, including their diet, digestion, and the degree of parental investment for their altricial young, several key differences distinguish these rabbit species. The most significant of these differences concerns the degree of sociality or gregariousness of the rabbits. *O. cuniculus* is a social animal that inhabits large communal warrens, whereas *S. floridanus* is a largely solitary animal. Indeed, Eastern cottontails are difficult to breed in captivity as they often fight when penned together, occasionally resulting in death (Dice, 1929).

Though both European and North American rabbits embarked on pathways to domestication, we suggest the behavioral qualities of European rabbits made them more susceptible to complete the path than eastern cottontails in two primary ways. First, the gregarious nature and ability to form stable social groups allowed European rabbits to be penned by humans and entire breeding populations could be managed within confined areas spaces with a minimal amount of inter-rabbit conflict. Enclosing eastern cottontails would have been more difficult due to their solitary nature and propensity to fight. Secondly, the natural tendency of European rabbits to form spatially clustered breeding groups centered on underground warren systems, would have allowed humans to easily locate, hunt, and eventually enclose and for managed breeding. New World cottontails, on the other hand, are solitary and more diffuse across a landscape making them harder to directly pen and manage.

In addition to their behavioral qualities, the overall diversity of rabbit species in North America may have served as a limiting factor for domestication. The fact that six different leporid species were found among the faunal bones at the Oztoyahualco compound of Teotihuacan indicates that residents practiced mixed acquisition and management strategies of diverse leporid populations rather than managing large breeding colonies of a singular species. Domestication requires a sustained multigenerational relationship with a specific animal population that has restricted gene flow with closely related wild populations (Larson and Fuller, 2014). The diversity of rabbits at Teotihuacan indicates that human residents had more extensive than intensive relationships with rabbits, a pattern not conducive to domestication. The biodiversity of North American cottontails may have thus acted to discourage the domestication of any singular species, despite direct human provisioning and management, and in spite of the importance of rabbits to human nutrition and culture.

Conclusion

In this article, we attempted to explain why though both Old World and New World rabbits embarked on pathways to domestication, only Old World rabbits obtained this status. We reviewed the archeological and historical evidence for the antiquity and intensity of human-leporid interactions in both Europe and North America, with an emphasis on new data from the archaeological site of Teotihuacan. We demonstrated that rabbits were dietary staples across large portions of North America and the Iberian Peninsula for many thousands of years. After reviewing the differing behavioral strategies of O. cuniculus and S. floridanus, we found that the social tendencies of these two species were the factors with the greatest divergence. Although O. cuniculus is gregarious and inhabits subterranean communal warrens, S. floridanus is solitary and their populations do not spatially cluster. Additionally, the biodiversity of rabbit species in North America encouraged humans to engage in extensive relationships with multiple leporid taxa rather than an intensive relationship with a singular rabbit species, as had occurred with O. cuniculus in Europe. We suggest that these factors made the European rabbit a more likely candidate for domestication than eastern cottontails.

Finally, the parallels observed in the human-rabbit relationships in Europe and North America challenge us to reconsider

About the Authors



Andrew Somerville is an assistant professor of anthropology in the Department of World Languages and Cultures University Iowa State at (ISU). He received a PhD in Anthropology from the University of California, San Diego, and spent a year as a UCMEXUS postdoctoral scholar at the National Autonomous University of Mexico in Mexico City. At ISU, he directs the Paleoecology

Laboratory and the Graduate Certificate Program in Forensic Sciences. His research focuses on understanding social-environmental dynamics of change in the pre-Hispanic Americas. **Corresponding author**: asomervi@iastate.edu

Nawa Sugiyama is an assistant professor at the University California, Riverside. She of applied zooarchaeological has and bone isotope methodologies to understand New World animal management strategies at Teotihuacan, Mexico, the Maya site of Copan, Honduras, and in various sites in Panama. Her research at Teotihuacan has covered topics pertaining to the construction of ritualized landscapes, human-animal interactions, and urban foodways. She is currently codirector of the Project Plaza of the Columns Complex.



the utility of the concept of domestication itself. For thousands of years and in both Europe and North America humans hunted, traded, and managed rabbits in captivity, but one rabbit population ultimately became the focus of intensive directed breeding by humans in southern France. Although all domesticated breeds today can be traced back to this small population, the archeological record demonstrates the rich history of human–rabbit interactions in Europe and North America. The observation that humans were moving, managing, and feeding populations of wild rabbits in multiple areas around the globe prior to the domestication of the European rabbit suggests that the binary distinction between wild and domesticated may fail to capture the complexities of many human–animal relationships.

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Feature Article

A workflow to design new directed domestication programs to move forward current and future insect production

Thomas Lecocq[®] and Lola Toomey

INRAE, URAFPA, University of Lorraine, Nancy, France

Implications

- Insect farming is expected to expand in the near future, but domestication is a long and difficult process which is often unsuccessful. Considering hits and misses from past directed domestications of insects and other species, we here provide a workflow to avoid common pitfalls in directed domestication programs.
- This workflow underlines that it is crucial to find relevant candidate species for domestication. Candidate species must address human need/ demand and meet a set of minimal requirements that shape their domestication potential. The domestication potential can be defined through an integrative assessment of key traits involved in biological functions.
- Geographic differentiation of key traits in a candidate species and the maintenance of adaptative potential of farmed populations should also be considered to facilitate domestication and answer to future challenges.

Key words: biodiversity, domestication, insects, integrative workflow

Introduction

Domestication has irrevocably shaped the history, demography, and evolution of humans. It is a complex phenomenon which can be seen as a continuum of relationships between humans and nonhuman organisms, ranging from commensalism or mutualism to low-level management (e.g., game keeping or herd management) or, even, direct control by humans over resource supply and reproduction (Terrell et al., 2003; Smith, 2011; Larson et al., 2014; Teletchea and Fontaine, 2014; Zeder, 2014, 2015). This continuum should not be seen as an obligatory succession of different relationships, which ultimately always ends by human control over reproduction, for all species involved in a domestication process. For instance, most fish domestications do not involve initial commensal relationships (Teletchea and Fontaine, 2014), and African donkeyowners do little to manage reproduction of African wild asses (Marshall et al., 2014). Moreover, it is worth noting that the domestication process 1) does not involve all populations of a particular species (e.g., some fish populations underwent domestication for aquaculture while wild conspecific populations still occur, Teletchea and Fontaine, 2014) and 2) is not irreversible (i.e., feral populations).

The complexity of the domestication process is mirrored by the diversity of past domestication histories. For instance, three main patterns of domestication histories can be identified for animal species: the "domestication pathways" (Zeder, 2012a, 2012b, 2015; Larson and Fuller, 2014; Frantz et al., 2016). The commensal pathway (e.g., dog and cat domestications) does not involve intentional action from humans but, as people manipulate their environment, some wild species are attracted to parts of the human niche, and commensal relationships with humans can subsequently arise for the tamest individuals of these wild species (Zeder, 2012b; Larson and Burger, 2013). Over generations, relationships with humans can shift from synanthropic interactions to captivity and human-controlled breeding (Larson and Fuller, 2014). The prey pathway (e.g., domestications of large herbivorous mammals) requires human actions driven by the intention to increase food resources for humans. The pathway starts when humans modify their hunting strategies into game management to increase prey availability, perhaps as a response to localized pressure on the supply of prey. Over time and with the tamest individuals, these game management evolve in herd management based on a control over movements, feeding, and reproduction of animals (Zeder, 2012a; Larson and Burger, 2013). At last, the directed pathway (e.g., domestication of transport animals, Larson and Fuller, 2014) is triggered with a deliberate and directed process initiated by humans in order to control movement, food supply, and reproduction of a wild species in captive or ranching conditions (Zeder, 2012a). All pathways lead to animal population evolution shaped by new specific selective pressures of the domestication environment (Wilkins et al., 2014). The divergence from wild ancestors further increases for species for which humans reinforce their control over population life cycle while they decrease gene flow between populations engaged in the domestication process and their wild counterparts (Teletchea and Fontaine, 2014; Lecocq, 2019). This control can ultimately result in selective breeding programs or organism engineering (e.g., genetically modified organisms) that are developed to

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intentionally modify some traits of interest (Teletchea and Fontaine, 2014; Lecocq, 2019).

Around 13,000 years ago, a first wave of domestication happened. It concerned mainly terrestrial vertebrate and plant species that are those dominating the agricultural world today (Diamond, 2002; Duarte et al., 2007). Noteworthy examples of insects involved in this wave include the silkworm (Bombyx mori, Lepidoptera) and the honeybee (Apis mellifera, Hymenoptera) (see domestication histories reviewed in Lecocq, 2019). Many insect domestication events started recently, in the 20th century (Lecocq, 2019), concomitantly with aquatic species (Duarte et al., 2007; Hedgecock, 2012) and some crop taxa (Leakey and Asaah, 2013), during the so-called new wave of domestication (i.e., refers to the large number of domestication trials since the start of the 20th century). Most domestications of this new wave follow a directed pathway through planned domestication programs (Duarte et al., 2007; Teletchea and Fontaine, 2014; Lecocq, 2019). This new wave has been facilitated by technological advances in captive environment control and animal food production. However, the triggering factor of this wave has been the emergence of new unmet human needs. Indeed, new domestication events appear unlikely when the human needs that could be met by targeted species (e.g., human food supply) are already addressed by wild or already domesticated species (Diamond, 2002; Bleed and Matsui, 2010; Freeman et al., 2015). For instance, many of the recent aquatic species domestications have been triggered by the need to meet the rising human demand for aquatic products while wild fishery catches are no longer sufficient (Duarte et al., 2007). Similarly, bombiculture (i.e., production of bumblebees, Hymenoptera, *Bombus* spp.) is an insect example of domestication triggered by an unmet human demand: the development of fruit production (e.g., tomatoes, raspberry) in greenhouses, which required importing insects such as bees to ensure the pollination ecosystem service. However, previously domesticated species, such as honeybees, are quite inefficient pollinators for such crops whereas bumblebees are ideal pollinators for these plants (Velthuis and van Doorn, 2006). This led to domestication of several bumblebee species since the 1980s (Velthuis and van Doorn, 2006). Overall, for insects, as for many other species, recent domestication programs have been triggered by needs to produce biological control agents (e.g., ladybugs, Coleoptera, Coccinellidae), pets (e.g., hissing cockroach, Blattodea, Gromphadorhina portentosa), and laboratory organisms (e.g., fruit flies, Diptera, Drosophila spp.), or for sterile insect technique development, and raw material/food production (reviewed in Lecocq, 2019).

New instances of insect domestication can be expected in the near future as several authors and international organizations claim that larger, optimized, and new insect productions will be a part of the solution to ensure human food/sanitary security and to address new demands for pets in the next decades (van Huis et al., 2013; Gilles et al., 2014; Lees et al., 2015; Mishra and Omkar, 2017; Thurman et al., 2017; Saeidi and Vatandoost, 2018). Here, we speculate that these future domestications will mainly follow a directed pathway as observed for other species involved in the new wave of domestication. These future domestication programs will be challenging since, despite technological developments, directed domestication is still a long and difficult process which often ends up being unsuccessful. Even when the life cycle is controlled by humans, major bottlenecks can still hamper the development of largescale production. Although limited amount of information about domestication failure rate is available in literature, past domestication programs of species involved in the new wave of domestication show that many new domestication programs often lasted a couple of years before being abandoned (e.g., for fish: Metian et al., 2019; for insect: Velthuis and van Doorn, 2006). The main causes of these failures are technical limitations, socioeconomic constraints, or intrinsic species features (Liao and Huang, 2000; Diamond, 2002; Driscoll et al., 2009). Potential solutions to facilitate domestication have been investigated for plants and vertebrates (e.g., Diamond, 2002; DeHaan et al., 2016; Toomey et al., 2020a). Conversely, insects have received very little attention to date (Lecocg, 2019).

Here, we consider feedbacks from past directed domestication programs of insects and other species to provide a conceptual workflow (Figure 1) to facilitate future insect domestication programs following a directed pathway (from this point, domestication will refer in the text to the directed pathway). This workflow ranges from the selection in the wild biodiversity of biological units (at species and intraspecific levels) to start new production to the development of selective breeding programs. We considered that technical limitations are not a major issue in insect domestication. Indeed, production systems (i.e., human-controlled environments in which animals are reared and bred) are already available for several phylogenetically distant insect species with different ecology, physiology, and behavior (Leppla, 2008). Thus, future insect domestications could likely be based, with potentially minor adjustments, on already existing production systems. Therefore, we here focus on how avoiding pitfalls due to socioeconomic constraints or intrinsic species features to move forward ongoing and future directed insect domestication programs to response to human demands.

Backing the Right Horse by Finding the Right Candidate Species for Domestication

Domestication processes which meet needs that can be more easily addressed by other means (e.g., wild catches or other domesticated species), as well as productions with a low productivity and/or profitability, are often doomed to failure (e.g., Diamond, 2002; DeHaan et al., 2016). Therefore, any new planned domestication program should consider how it could respond to an unmet human requirement with a viable and efficient business model. This can be at least partially answered by an evaluation of potential candidate species for domestication before starting large-scale production.

First: identifying an unmet human need or demand to define new candidate species

Human need or demand can focus on a species of interest (species-targeted domestication). Such domestications happen


Figure 1. A seven-step workflow to develop a fruitful insect production. 1. Identification of an unmet human demand. 2. Identifying candidate species that could meet the demand through a multifunction and multitrait assessment jointly developed with stakeholders. 3. Decision-making rules established with stakeholders highlight species with high domestication potential (here, one species but several species can be chosen). 4. Investigating the interest of geographic differentiation between wild populations (prospective units) of the species, similar to steps 2 and 3 to highlight units with high domestication potential (two units in this fictive example). 5. Creating the initial stock through pure or cross breeding strategy with attention paid to the genetic diversity of this stock (here, a cross breeding strategy is used). 6. Initial stock improvement through selective breeding programs and/or wild introgression to minimize adverse effects and reinforce beneficial domestication effects. 7. Production evolution according to human demand and environmental changes thanks to its adaptive potential and methods developed in the previous step. When no adaptation can be developed, new domestication could be considered. Wild biodiversity is considered at the species and intraspecific levels.

1) when a wild species already exploited by humans becomes rare (e.g., for insects see Lecocq, 2019) or protected (e.g., the European sturgeon, Actinopterygii, *Acipenser sturio*) in the wild, 2) to allow reintroduction for wildlife conservation (e.g., for butterflies, Crone et al., 2007), or 3) to develop sterile insect techniques (see Lecocq, 2019). At this stage, the species of interest is regarded as a candidate species that must be further studied to assess the feasibility of its domestication (Figure 1).

The need or demand for a particular ecosystem service can also spark new species farming (service-targeted domestication, see also DeHaan et al., 2016), as exemplified by bumblebee domestication (Velthuis and van Doorn, 2006). Since most ecosystem services can be ensured by numerous taxa, several candidates for domestication could be identified. This raises the need to highlight among available candidates those that maximize the chance of success to go successfully through the domestication process (DeHaan et al., 2016).

Second: the importance of an integrative assessment of candidate species

Before going any further in the domestication program development, special attention should be paid to international and national regulations regarding sampling, transport, and use of candidate species. Indeed, such regulations can prevent producing or trading a species in some areas (e.g., Perrings et al., 2010; Samways, 2018), making its domestication economically poorly attractive or pragmatically useless. They can thus limit the number of potential candidates or make a species-targeted domestication unfeasible.

Wild insect species are not all suitable candidates for domestication. Indeed, each species has a specific "domestication potential" (adapted from Toomey et al., 2020a): a quantification of how much expression of key traits is favorable for domestication and subsequent production. Several behavioral, morphological, phenological, and physiological key trait expressions have been highlighted as relevant to facilitate domestication and subsequent production (e.g., for noninsects, Diamond, 2002; Driscoll et al., 2009). By considering insect specificities, we state that these expressions include high growth rate, high food conversion ratio, generalist herbivorous feeder or omnivorous, high survival rate, short birth spacing, polygamous or promiscuous mating, large environmental tolerance, high disease resistance, gregarious lifestyle, and diet easily supplied by humans. This list should be completed with additional key traits specific to the domestication purpose. For instance, pollination efficiency is relevant for pollination-targeted domestication while nutritional quality is important for edible insect domestication. Moreover, expression of socioeconomical key traits must also be considered for domestication potential assessment such as high yield per unit, high sale value, established appeal for consumers, and useful byproducts (e.g., for silkworm; Lecocq, 2019). At last, potential environmental consequences of future production, such as risks of biological invasions associated to the development of international trade (Lecocq et al., 2016), should be considered through the evaluation of relevant traits (e.g., invasive potential, which corresponds to the ability of a species to trigger a biological invasion out of its natural range). Overall, the set of key traits can be defined thanks to advice or expectations of stakeholders (consumers, environmental managers, policy makers, producers, and socioeconomists) (Figure 1; see similar approach for fish in Toomey et al., 2020a).

It is worth noting that key traits 1) are involved in different biological functions (behavior, growth/development, homeostasis, nutrition, reproduction) and 2) are not necessarily correlated among each other, implying that expression of a trait cannot be inferred from other traits (Toomey et al., 2020b). This means that species domestication potential must be assessed by a multifunction and multitrait integrative framework (Figure 1). Moreover, species might present specificities in the wild but those might not be maintained in production systems because expression of key traits, as any phenotypic trait, is determined by genetic divergence and environment, as well as the interaction between these two factors (Falconer and Mackay, 1996). Therefore, an efficient assessment should be performed in experimental conditions as close as possible to the production system. Overall, such an assessment can be seen as heavy-going and time- and money-consuming. However, the complexity of multifunction and multitrait assessment in standardized conditions is offset by the minimization of the risk to start a long and difficult domestication program with the wrong candidate species.

Third: reaching a consensus to choose relevant candidate(s) to start domestication

Making an integrative assessment of domestication potential should not hide the fact that some key traits can be more important than others. For instance, very low survival rate or low reproduction rate during the assessment will certainly stop ongoing domestication trials because they prevent the completion of the life cycle. Therefore, minimal expression threshold (i.e., minimum threshold for a trait expression which must be met or else the biological unit is not suitable for domestication programs; e.g., a survival rate below which an animal production would not be economically feasible) should be defined, potentially by a panel of stakeholders, for the most important traits relatively to the domestication purpose (see similar approaches in DeHaan et al., 2016; Toomey et al., 2020a). When a species does not meet this threshold, it must be regarded to be void of domestication potential. This threshold must be carefully defined, even in species-targeted domestication programs, to avoid starting large-scale domestication programs with issues that could be costly and slow or impossible to fix later in the process.

When comparing key trait expressions between species, it is likely that a candidate displays a favorable expression for a specific key trait (e.g., best nutritional value) but not for another trait (e.g., lowest survival rate). This requires making a consensus between results of key trait assessment to identify the best candidate species for a service-targeted domestication or to objectively assess the relevance of a species-targeted domestication (Figure 1, e.g., for noninsect species, Quéméner et al., 2002; Alvarez-Lajonchère and Ibarra-Castro, 2013; DeHaan et al., 2016). Scoring solutions could be used, considering weighting coefficients to integrate the potential differential levels of importance of key traits due to socioeconomic factors, absolute prerequisites for domestication, or production constraints. Weighting coefficients can be defined through surveys of stakeholders' expectations (Figure 1; see examples in Quéméner et al., 2002; Toomey et al., 2020a). Since expectations might vary across stakeholders, decision making should be based on a consensus between all parties involved (see strategies to solve complex scientific and socioeconomic issues and consensus solutions in Hartnett, 2011; Wyborn et al., 2019; Toomey et al., 2020a). Ultimately, weighted integrative assessment of candidate species allows highlighting those that would likely foster new fruitful domestication programs for servicetargeted domestication or confirm/infirm the relevance of a species-targeted domestication process. These candidates are thus called species with high domestication potential.

Getting Off on the Right Foot Thanks to Intraspecific Diversity

Fourth: having the best intraspecific unit to start new domestication programs

Once a new species with high domestication potential has been identified, considering geographic differentiation between allopatric groups of conspecific populations (commonly observed in insects; e.g., Araki et al., 2009; Uzunov et al., 2014) can be helpful to further facilitate domestication programs (Toomey et al., 2020a). Indeed, such population groups can present divergent demographic histories, which can shape genetic and phenotypic specificities through 1) gene flow limitation or disruption, 2) random genetic drift, and/or 3) local adaptation (Mayr, 1963; Avise, 2000; Hewitt, 2001; Toomey et al., 2020a). This could ultimately lead to differentiation in key traits and, thus, to divergent domestication potentials between wild population groups. A few past domestication histories show that geographic differentiation can facilitate domestication (e.g., for fishes: Toomey et al., 2020a; for crops: Leakey, 2012; Leakey et al., 2012). In insects, the domestication of the buff-tailed bumblebee (Hymenoptera, Bombus terrestris) is one of the few stunning examples where populationspecificity inclusion in domestication programs fostered a fruitful economic development. The buff-tailed bumblebee displays significant differentiation in key traits (e.g., foraging efficiency, colony size, and diapause condition) between differentiated groups of populations corresponding to subspecies (Velthuis and van Doorn, 2006; Kwon, 2008; Lecocq et al., 2016). In the early years of production, European bumblebee breeders tried to domesticate several subspecies. Within a short space of time, one subspecies (B. terrestris dalmatinus) proved to have superior characteristics from a commercial point of view (i.e., largest colonies, efficient highest rearing success rate, high pollination efficiency) and became the dominant taxa in the bombiculture industry (Velthuis and van Doorn, 2006). Similarly, non-African honeybees were favored for domestication and production due to facilitating key traits (e.g., low tendency to swarm, survival in temperate areas, low aggressiveness) for beekeeping over African honeybees (Wallberg et al., 2014).

Potential importance of geographic differentiation for insect domestication programs raises the question about how it should be integrated in domestication processes. To this end, a new integrative approach has been recently developed for fish domestication (see Toomey et al., 2020a). This approach provides an integrative assessment of differentiated allopatric population groups through three steps (Figure 1). The first step aims at classifying wild populations of a targeted species in prospective units through phylogeographic or systematic methods. These units are groups of allopatric populations that are likely differentiated in key trait expressions. The second step provides an integrative multifunction and multitrait assessment, similar to interspecific comparison of domestication potential but applied to prospective units. Finally, the last step highlights prospective units with higher domestication potentials (so-called units with high domestication potential, UHDP) through the calculation of a domestication potential score through the help/advice from stakeholders (see Toomey et al., 2020a).

Fifth: constituting the best stock to start new domestication programs

When several UHDP are highlighted as of interest, the question can be raised regarding which strategy should be adopted to constitute the initial stock (Figure 1): 1) keeping only one UHDP or breeding several UHDP apart ("pure breeding" strategy) or 2) mixing UHDP ("cross breeding" strategy) (Falconer and Mackay, 1996). Pure breeding consists of starting with one biological unit and continuously improving it through time (e.g., for *B. terrestris*, Velthuis and van Doorn, 2006 or A. mellifera, Uzunov et al., 2014). It is an effective strategy when one biological unit presents a much higher domestication potential than others. In contrast, crossbreeding could be an interesting alternative (e.g., see trials with tasar silkworm, Lepidoptera, Antheraea mylitta, Lokesh et al., 2015) when several units present a similar domestication potential or complementary interests. It consists of crossing two or more biological units aiming at having progeny with better performances than parents through complementary of strengths of the two parent biological units and heterosis (i.e., hybrid vigor). However, it is a hit-or-miss strategy since results are hardly predictable (e.g., negative behavioral consequences in A. mellifera crossings, Uzunov et al., 2014). The choice regarding which strategy should be used must made on a case-by-case basis.

Further attention should be paid to genetic diversity when constituting the initial stock (Figure 1). If this stock is constituted with a low number and/or closely related individuals, the resulting low global genetic diversity of farmed populations will quickly lead to inbreeding issues, which can be especially damaging in some insect groups such as Hymenoptera (Gerloff and Schmid-Hempel, 2005). It is even more important in the pure breeding strategy which most likely leads to a lower initial genetic diversity than cross breeding approaches. Therefore, care should be taken that a sufficient number of individuals/families (i.e., sufficient effective size) is considered (i.e., sampling strategy) to 1) have a sufficient initial genetic variability and avoid to sample kin individuals which increase risks of future inbreeding issues, 2) mitigate the risk of sampling suboptimal genotypes which are not representative of the population group, and 3) have a sufficient genetic variability for future selective breeding programs (Toomey et al., 2020a).

Going Further in the Domestication Process: The Wise Way

Sixth: improving stocks undergoing domestication

During domestication, farmed populations undergo new selective pressures from the rearing environment, a relaxation of wild environmental pressures, and other genetic processes, such as founder effect, genetic drift, or inbreeding (Wilkins et al., 2014). These processes lead to genetic, genomic, and phenotypic differentiations (Mignon-Grasteau et al., 2005; Wilkins et al., 2014; Milla et al., 2021), which are overall poorly studied in insects compared with other taxa (Lecocq, 2019). Yet, they can trigger changes in key trait expressions that are often observed in domesticated species (e.g., for insects: higher tameness, lower aggressiveness toward humans and conspecifics (Latter and Mulley, 1995; Adam, 2000; Krebs et al., 2001; Zheng et al., 2009; Chauhan and Tayal, 2017; Xiang et al., 2018). These changes can facilitate domestication or lead to an improvement of performances (i.e., beneficial changes) that enhances the profitability of the production sector (e.g., higher silk production in silkworm; Lecocq, 2019). However, some changes can also be unfavorable for domestication and subsequent production (i.e., adverse changes) as shown in other taxa (e.g., reproduction issues in fish, Milla et al., 2021).

Selective breeding programs are widely used as a solution to overcome adverse changes or reinforced beneficial changes shaped by domestication (Figure 1). The efficiency of such programs was demonstrated for several taxa (e.g., broiler chicken, Gallus gallus domesticus, Galliformes, Tallentire et al., 2016, Atlantic salmon, Salmo salar, Salmoniformes, Gjedrem et al., 2012), including insects (e.g., Adam, 2000; Simões et al., 2007; Zanatta et al., 2009; Bourtzis and Hendrichs, 2014; Niño and Cameron Jasper, 2015). Despite the success of numerous breeding programs, they can also lead to negative-side effects. This is well known in livestock (Rauw et al., 1998) but it was also investigated in insects (e.g., Oxley and Oldroyd, 2010). An alternative solution to solve deleterious changes shaped by domestication relies on introgression of wild individuals in farmed populations (Figure 1, Prohens et al., 2017). For instance, in insects, a hybridization was performed between wild African and domesticated European A. mellifera populations to create an Africanized strain which would be better adapted to tropical conditions and present a higher honey production (Spivak et al., 2019). However, despite its efficiency for honey production, its defensive behavior quickly became an issue and is considered nowadays as a matter of concern in Americas (Spivak et al., 2019). Overall, the development of selective breeding programs or wild introgression in insect domestication could be of great interest but attention should be paid to traits selected and to potential negative consequences.

Seventh: keeping one step ahead by maintaining the adaptive potential of production

The relevance of an insect production depends on the socioeconomic and environmental contexts which can change over time. First, the triggering factor of domestication events, the human demand/need, can change with time and/or additional demands can appear aside from the original ones due to market fluctuations, new regulations, or technological development. Second, ongoing global changes (e.g., global warming, pollution) can impact production systems (i.e., outdoor production) and/or availability of important resources for farming (Decourtye et al., 2019). This places a premium on maintaining the adaptive potential of insect production over time, jointly with stakeholders, through species intrinsic features, selective breeding programs, wild individual introgressions, or new domestication program developments (Figure 1).

Insect farming can face these changes thanks to species intrinsic features such as large climatic tolerance or generalist diet. In the context of global changes, the ability to cope with environmental changes is thus a valuable information that should be considered early in the process, during the assessment of candidate species domestication potential (see examples of species-specific responses to climate change or abiotic parameters between closely related species in (Oyen et al., 2016; Martinet et al., 2020).

Alternatively, insect productions can evolve to deal with socioeconomic and environmental changes through selective breeding programs (i.e., continuous adaptation) to improve farmed populations (through trait selection or wild introgression) or create new specialized strains (Decourtye et al., 2019). However, selective breeding programs often drive to a loss of genetic diversity, which can trigger a lower resilience of farmed stocks (Gering et al., 2019). Indeed, genetic variability defines a biological unit's ability to genetically adapt to future challenges and contributes to global species biodiversity, which maximizes species survival chances in the long term (Sgrò et al., 2011). This appears even more important considering that some rearing practices can quickly lead to a loss of genetic variability (e.g., beekeepers specializing in queen breeding and consequently a large amount of progeny originate from a few queen mothers, Meixner et al., 2010). Moreover, genetic variability can also be important for the population fitness (e.g., this variability is essential for disease resistance and homeostasis in A. mellifera, Meixner et al., 2010). Overall, the maintenance of genetic variability is capital (Figure 1) and could be facilitated by wild introgressions (Prohens et al., 2017).

Finally, in extreme cases in which farmed stocks cannot face/be adapted to new socioeconomic and environmental contexts, it will be necessary to start new domestication programs using new candidates (new wild species or population groups).

Conclusion

Insect farming is expected to expand in the future but remains challenging because of the difficulty to domesticate new species. We proposed a conceptual workflow to avoid major problems commonly encountered during domestication programs. We underlined the importance of 1) considering how new species production could respond to an unmet human demand with a viable and efficient business model and 2) assessing the domestication potential of candidate species through an integrative assessment. We argued that geographic differentiation between wild populations of a candidate species can be valuable. At last, we emphasized the importance of maintaining the adaptive potential of productions to answer to current and future challenges.

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About the Authors



Thomas Lecocq-He is an associate professor (senior lecturer) in animal biology and ecology. He works on functional ecology, ecological niche modeling, systematics, and phylogeography. His current research projects focus on the development of integrative and conceptual approaches to support domestication programs. He explores how intraspecific diversity and interspecific interactions can facilitate domestication process and increase animal production sustainability. Corresponding author: thomas. lecocq@univ-lorraine.fr

Lola Toomey—After obtaining a MSc in marine biology at the University of Western Brittany (France), she received her PhD in agronomy from the University of Lorraine (France). Her PhD research focused on the integration of geographic differentiation in domestication programs to promote aquaculture diversification. Her current research interests include population genetics, phylogeography, domestication, and agronomy.



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Perspectives

The origins of the domesticate brown rat (*Rattus norvegicus*) and its pathways to domestication

Ardern Hulme-Beaman,[†] David Orton,[‡] and Thomas Cucchi^{||}

[†]Department of Archaeology, Classics and Egyptology, University of Liverpool, 12–14 Abercromby Square, Liverpool, L69 7WZ, UK [‡]BioArCh, Department of Archaeology, University of York, York YO10 5DD, UK

^{II}Archaeozoology, Archaeobotany, Societies, Practices, Environments (AASPE-UMR7209), CNRS, National Museum of Natural History (MNHN), Paris, France

Implications

- Historical evidence indicates that brown rats went through a series of human-influenced and/or controlled-breeding events at different times and locations: Japan in the 1600 to 1700s, Europe in the early 1800s, and North America in the mid-1800 to early 1900s.
- The European and Japanese controlled-breeding events may be considered domestication events, whereas the later events from the mid-1800s onward might be considered selective breeding of an already domesticated animal.
- Each event appears to have been for a different purpose: Japanese rats were pets and ornamental; early European breeding was in the first instance for blood sports and food sources for captive carnivores; North American selective breeding was for laboratory use.
- Modern examination of domestic brown rats has almost exclusively focused on laboratory strains, which stem from a limited source and there has been little to no exploration of pet or fancy rat populations.

Introduction

The brown rat (*Rattus norvegicus*) is one of the most pervasive and familiar species across the globe. Its familiarity in society and experimental lab work belies a complex history (Figure 1), which is exemplified by its contradictory name; it is not always brown as additional color morphs regularly occur in some populations (Aplin et al., 2003), and there is no fossil evidence for any *Rattus* species from Norway, from which its binomial "*norvegicus*" derives (Berkenhout, 1769; Lindsey and Baker, 2019). Biologically, it is extremely well understood as it forms one of the major mammalian model lab species and

doi: 10.1093/af/vfab020

is only rivaled by the mouse (*Mus musculus*) (Hedrich, 2019). However, extraordinarily little is known about the brown rat's native origins and natural/wild behaviors (Hulin and Quinn, 2006; Ness et al., 2012; Zeng et al., 2018). The vast majority of research conducted on this species is focused on laboratory work and observations of behaviors in domestic and laboratory populations; wild studies are almost exclusively focused on invasive commensal populations and those occupying human environments where ecological pressures and competitive interactions with other species differ from its likely native range (e.g., ecological and evolutionary studies such as Figgs, 2011; Kajdacsi et al., 2013; Puckett and Munshi-South, 2019). As such the dispersal history, evolution and origins of the brown rat in the lead up to and eventual domestication are all in considerable need of investigation. Here we provide a brief review of this biologically important and ecologically influential species and examine the processes by which it was domesticated.

Brown Rat Origins

The origins of the brown rat are far from clear with its earliest association with humans obscured by a lack of direct evidence. Fossil evidence for the brown rat is scarce, as it is for many species of the Rattus genus, and identification of fossil specimens to species level can be extremely challenging (Pagès et al., 2010; Hulme-Beaman et al., 2019). The divergences of R. norvegicus, its natural ecology and indigenous precommensal range are subject to much uncertainty as a result (Hedrich, 2019). Genetic evidence suggests that the brown rat diverged from the other major Eurasian Rattus species between 0.9 and 2.9 million yr ago (Teng et al., 2017; Zeng et al., 2018), sometime between the early and middle Pleistocene. Genome-wide studies of the brown rat and its sibling species the Himalayan field rat (Rattus nitidus) indicate these two species diverged sometime in the Middle Pleistocene following large-scale climate fluctuations, but that early divergence was followed by extensive and multiple introgression events (Teng et al., 2017). Middle to late Pleistocene evidence for Rattus spp. extends across Eurasia, with a Rattus species (Rattus cf. haasi) present in the eastern Mediterranean up until at least the Last Glacial Maximum (LGM) (e.g., in the Zuttiyeh cave,

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Israel: Tchernov, 1968; Yarimburgaz Cave, Turkey: Santel et al., 1998; Qesem Cave, Israel: Maul et al., 2016). However, both the dating and the taxonomic relationship between the modern brown rat species and these Pleistocene rats remains unclear (Tchernov 1968). Some fossil evidence also identifies the presence of the brown rat (stricto sensu *Rattus norvegicus*) in southern China during the middle and late Pleistocene (Wu and Wang, 2012), but it is unclear how these fossil specimens compare with closely related species such as *R. nitidus*, which is often described as having a more southerly range (Aplin et al., 2003).

The indigenous distribution of the brown rat is often cited as the northern regions of China, Mongolia, and/or south-eastern Siberia (Figure 1), and its ability to survive well in temperate climates is used to support this (Hedrich, 2006; Puckett et al., 2016). Although not explicitly stated, reference to indigenous range in most modern studies probably refers to its natural range after the LGM, as climate and environment in the northern region of China has changed considerably over the late Pleistocene and Quaternary (Yang et al., 2004). Discussions of the brown rat's temperate climate adaptations and native range, however, do not appear to consider paleoclimates directly. There is a large gap in the record and knowledge surrounding the period and process during which the brown rat adapted to human environments in Chinese prehistory (see below). From its native distribution in East Asia, the brown rat was later transported globally, most likely on ships (Puckett et al., 2020). This appears to have occurred sometime in the 1700s based on European and North American documentary accounts (Hedrich, 2019) and has led to a global distribution with multiple invasive and commensal populations. In large part, efforts to model brown rat native distributions are hampered by an inability to robustly assess which commensal and translocated populations are surviving in extreme climates because of human resource exploitation and which populations could survive such climates in the absence of humans.

A number of different genetic studies conducted on modern specimens have suggested varying commensal and precommensal origins within East Asia, including both Southeast and/or Northeast Asia (Song et al., 2014; Puckett et al., 2016; Zeng et al., 2018; Puckett and Munshi-South, 2019), but those studies do not include any ancient specimens. As such, the native range of the brown rat remains debated, but generally restricted to eastern Asia. Genomic analyses have also been used to identify probable demographic expansions that might be associated with advances into human-commensal niches and further translocation events (Zeng et al., 2018; Puckett and Munshi-South, 2019). However, the results vary widely with some suggestions of expansions dating to ~800 BP (Puckett and Munshi-South, 2019) and others of expansions dating much earlier to between 3000 and 1800 BP (Zeng et al., 2018). These early dates of expansion do not at all match historical accounts of new arrivals of rats to Europe in the 1700s, which describe in some detail a new species of larger rat aggressively competing with and extirpating existing rat populations in France, England, Ireland, and Denmark (Buffon, 1760; Pennant, 1768; Rutty, 1772; Smith, 1772; Winge, 1908 referring to notes from 1755 by Urne). Without ancient specimens, these genetic studies remain limited and robust species divergence dates and assessment of native ranges, pre- and post-LGM, will remain poor until evidence is bolstered by extensive and combined zooarcheological and ancient DNA analyses (e.g., as has been done with mice; Cucchi et al., 2020).

Earliest Archeological Evidence

Archeological evidence for the brown rat is extremely poorly documented (Armitage, 1994; Ervynck, 2002). This is largely



Figure 1. Map indicating the assumed native distribution of *Rattus norvegicus* (in blue) and locations of major rat domestication processes (marked with depictions). From East to West: Hooded rat depiction adapted from an image within the 1700s Japanese rodent breeding guide book, the *Chinganso-date-gusa* (1787); Rat-baiting dog depiction adapted from Mayhew (1851) *London labor and the London poor* illustrating blood sport activities from which European domestic rats arose; laboratory rat silhouette representing the postdomestication selective breeding of rats for laboratory inbred strain development at the Wistar Institute of Philadelphia in the early 1900s.

due to the brown rat's innate fossorial (burrowing) behavior, which leads to it being a major contaminant in archeological contexts and a general source of taphonomic disturbance (Armitage, 1994). Added to this are the difficulties of identification with regards to other commensal rats: although intact crania of black and brown rats are readily distinguishable. metrical indices on the mandible (Armitage et al., 1984) show overlap between species (Walker et al., 2019), and postcranial morphological criteria (Wolff et al., 1980; Ervynck, 1989) are relatively unreliable (Koski, 2019). Although black rats are typically significantly smaller than brown rats when the two are found in the same environment, the former may be larger-and may exploit a wider niche-when the latter is absent (Ervynck, 1989; Armitage, 1994). The resulting variability and potential overlap renders size an unreliable criterion for distinguishing archeological specimens. The identification of fossil specimens of *Rattus* species is particularly difficult, especially in regions where multiple *Rattus* species are sympatric (Hulme-Beaman et al., 2019); this is well demonstrated by the regular occurrence of misidentification of Rattus species in modern field caught studies and museum collections (Pagès et al., 2010).

The earliest record of brown rats in archeological contexts confirmed with advanced morphological analyses (geometric morphometrics) derive from central or northern China dating to the early Neolithic and the development of agriculture (7000 to 9000 BP—A. Hulme-Beaman et al., in preparation). These were found in direct association with humans and human refuse middens, which indicates a likely commensal relationship for this population. The next archeological evidence for commensal brown rats, secure both in dating and taxonomic identification, is distant in time and space from the species' native range, deriving from an 18th-century shipwreck off the coast of Corsica (Vigne and Villié, 1995). Earlier reported European finds, such as at 14th-century Tarquinia, Italy (Clark et al., 1989), require direct dating and confirmation of taxonomic identity. For now, the early direct evidence for the emergence of commensal behaviors in brown rat populations is extremely limited, and the process of adaptation to human environments is poorly understood. There is no direct archeological evidence for the domestication of brown rats or their maintenance in captivity; historical accounts of rat keeping and breeding are therefore the best evidence for itsdomestication.

The Domestication of the Brown Rat

The pathway to domestication (see Sidebar 1) for the brown rat might not be so clear as it first seems given selective breeding of rats for laboratory use and its intense commensal relationship with humans. In addition to breeding in close association with humans in commensal populations, the brown rat was managed and deliberately bred in controlled circumstances or direct captivity under at least three different conditions and similarly for three different purposes: rat-baiting rats (Mayhew, 1851), fancy rats (Kuramoto, 2011), and biomedical laboratory rats (Richter, 1954) (Figure 1). Each different purpose could align somewhat with a different proposed pathway

Sidebar 1. Pathways to domestication

Within studies of the process of domestication, three major pathways have been proposed (Zeder, 2012): commensal pathway; prey pathway; and directed pathway. Each of these pathways has a different starting point and likely initiated by different agents in the process. The commensal pathway to domestication is initiated by the nonhuman agent in the process and occurs when other animals are attracted to human environments and undergo a prolonged period of habituation with humans; an example of this might be the cat whereby the progenitors of modern domestic cats might have been attracted to human environments due to human resources or the other commensal species that consume them. Other possible examples of the commensal pathway to domestication include the pig and the dog (Zeder, 2012). The prey pathway to domestication occurs with initiation by humans and is primarily focused on large prey species and occurs when humans increasingly manage wild game by encouraging their proliferation and then changing their demographics; this culminated eventually in determining which animals breed through herd management. It is thought to have likely occurred in the domestication of sheep (Ovis aries), goats (Capra hircus) and cattle (Bos taurus). Finally, the directed pathway to domestication is primarily instigated and managed by humans and involves the specific selection of individuals for breeding; once humans have an idea and familiarity with other domestic animals then directed pathway domestication can occur rapidly, with deliberate purpose. Animals that might have followed the directed pathway to domestication are recently domesticated species such as foxes (Vulpes vulpes), mink (Mustela vison) and chinchilla (Chinchilla lanigera). These pathways are not strict and aspects of each may cross over, but each may come with its own underlying selective pressures, which might then influence the course of their domestication.

to domestication as the selective pressures would be different under each circumstance (Zeder, 2012). An important factor in this is also the possibility of different pathways to domestication occurring for different populations of rats in space and time. This is most notable in the domestication of brown rats whereby major laboratory strains come from different populations bred into inbred laboratory strains at different times.

The earliest evidence for a form of rat domestication comes from Japan where a tradition of keeping fancy rats emerged during the Edo period (1603 to 1868) (Serikawa, 2004; Hedrich, 2006). It is likely that these fancy rats derived from the brown rat (Serikawa, 2004; Hedrich, 2006; Kuramoto, 2011), though other species cannot be fully discounted (e.g., the Asian house rat [Rattus tanezumi] or another rat within the Rattus rattus species complex) because modern remnants of these Japanese fancy rats have not been identified (Kuramoto, 2011). It is also not clear as to whether Japan is part of the species' native range or whether they arrived as commensal animals and if so, when this was. However, the early breeding of rats in Japan is very clearly demonstrated by two early breeding guides dating to the late 1700s (the Yoso-tama-no-kakehashi of 1775 and the Chinganso-date-gusa of 1787, Figure 2A), and many of the color morphs and patterns described are found in domestic brown rats today (Kuramoto, 2011). The early documentation of Japanese rodent breeding indicates that such breeding had been carried out as early as 1654 (Serikawa, 2004; Hedrich, 2019). There is also some indication that similar fancy rat breeding took place in China around the same time, or even



Figure 2. Panel of domestic rats. (A) Composite image of rat and mouse keeping cages from the *Yoso-tama-no-kakehashi* (1775) and four images of different color morphs of rats from the *Chinganso-date-gusa* (1787). (B) Rat-baiting event depicted from Mayhew (1851) London labor and the London poor. (C) Three female fancy rats displaying gregarious social behavior (photo credit Robert Lachlan).

possibly earlier, with old Chinese stories about fancy rodent breeding referred to in *Yoso-tama-no-kakehashi* (Kuramoto, 2011), but the direct relationship of these stories to specific breeding or domestication and the early occurrence of this needs further exploration. Furthermore, there are descriptions in the *Chinganso-date-gusa* of fancy mice being traded to Japan (Yonekawa et al., 1982) and as a result, the possibility of earlier fancy rat breeding in China cannot be excluded. This occurrence of rat domestication with specific selection for certain desirable traits might be considered to fall under the "directed pathway" to domestication, whereby people could have used their prior knowledge of management of domestic animals to "fast-track" the domestication process (Zeder, 2012).

Given Japanese isolation under the policy of *sakoku* from the 1630s to 1853, these fancy rats are unlikely to have contributed to rat populations elsewhere before the late 19th C, if at all—although commensal rats from Japan may have spread to the Aleutians via a shipwreck as early as 1780, according to a Russian account from 1826/1827 (Khlebnikov, 1979). Trained rats were displayed in Paris in 1667 according to the revised German edition of Gesner's *Historia Animalium* (Gesner and Horst, 1669), but this anecdote appears in the entry on *mure domestico majore*, conventionally taken to refer to the black rat. Writing in Paris almost a century later, Buffon (1760) noted that it was "only nine or ten years" since the brown rat had appeared in the environs of the city.

Rats have also been kept as food and sport animals, though not for human consumption, and it appears that the process of managing such stocks may have given rise to most modern domestic rats (Lindsey and Baker, 2019). Within England, France, and later North America, brown rats were regularly bred from the early 1800s for sport with dogs in rat-baiting events (Richter, 1954); a single dog could kill up to 100 rats in a single timed round (Figure 2B, the number often decided by the dogs weight; Drabble, 1948) and, as such, large numbers were required (Mayhew, 1851). Albino individuals were removed from this breeding process and kept separately for show and further selective breeding (Mayhew, 1851), and Richter (1954) suggests that many modern domestic rats derived from this stock.

Some further accounts from rat catchers and fancy rat breeders in the London area in the 1800s suggest albino rats were wild caught, with one rat catcher, Jack Black, describing catching his first white rat wild in Hampstead, UK, and catching black color morphs in Regent Street, London, before breeding directly from them (Mayhew, 1851). Notably, Jack Black reports selling his tame and fancy rats widely and even internationally, with some 300 being sold to buyers in France (Mayhew, 1851).

Amongst the earliest captive rat closed colonies (i.e., those that are self-sustaining and not replenished with new animals) are those recorded from 1856 in the Jardin des Plantes, Paris (Lindsey and Baker, 2019). This colony was noted as consisting of hooded brown rats (white with a black head), was set up to feed the reptiles housed in the gardens, and was maintained until 1988 (Hedrich, 2019). Its foundation date closely matches that of the rat-baiting events and early selective breeding of the 1800s (Mayhew, 1851), so could follow Richter's (1954) interpretation that modern stocks derive from such activities. As the colony consisted of individuals with a nonwild color morph, this population had probably undergone a number of selective breeding events already, reflecting the activities of local fancy rat breeders (Mayhew, 1851). This colony was not selectively bred for laboratory use though until much later and it was only in the 1980s that rats from it were taken and developed into an inbred laboratory strain for experimentation (Hedrich, 2019). Having been initiated via direct capture by humans, this process has obvious parallels to the Japanese fancy rats and the "directed pathway" to domestication. Yet in terms of population management for rapid consumption, and the indirect selective pressures likely to have been experienced by these managed populations, this domestication process arguably has some commonalities with the "prey pathway" (cf. Zeder, 2012).

Brown rats were among the earliest mammal species used specifically for laboratory experiments (Richter, 1959). The earliest use of the brown rat as a laboratory animal appears to have emerged in the early 1800s with the use of albino brown rats in dietary studies (Savory, 1863) and studies of the adrenal glands (Philippeaux, 1856). From that point onward, the brown rat was used in a range of different studies including specific breeding experiments in the late 1800s (Crampe, 1877, 1885), presumably with animals originating from rat-baiting activities. By the early 1900s, Henry H. Donaldson at the Wistar Institute of Philadelphia began the first breeding programs to establish specific laboratory inbred rat strains (Hedrich, 2019). Therefore, although there were closed colonies prior to 1900 such as that of the Jardin de Plantes, they were not bred with intent for laboratory purposes and it is only with the rat strain developed by Henry H. Donaldson that the first laboratory rats emerged. Even though the brown rat is often cited as being domesticated as a laboratory animal (e.g., Richter, 1959; Gibbs et al., 2004), from the perspective of wider domestication studies it might be considered that the specific breeding of rats for laboratories was largely secondary to the initial domestication process, which appears to have commenced with stock management and breeding of fancy rats (e.g., Mayhew, 1851). Breeding rats for laboratory use therefore is more comparable with the breeding of dogs for specific roles in human society and probably started with a rat population that had already been selectively bred and in some cases was maybe even docile.

Origins of Modern Domestic Lineages

A number of genetic studies have been carried out on the different lineages of domestic rats to understand their relatedness (Canzian, 1997; Thomas et al., 2003; Puckett et al., 2018). Those genetic studies found that there is a large amount of genetic diversity amongst the domestic strains (Canzian, 1997; Thomas et al., 2003), though notably not nearly as much as in domestic mouse populations (Ness et al., 2012). In particular, these studies found that the strains from the likely oldest closed colony in the Jardin de Plantes are the most divergent (Canzian, 1997). This would further suggest multiple domestication events or early separation of breeding lineages. More recent work examining nuclear genomes at higher resolutions suggests the diversity found within combined inbred strains is moderate relative to the diversity within wild populations (Puckett et al., 2018). This study also found all laboratory strains examined (25 of >500) derived from a single ancestral source from a likely small and unknown geographic region (Puckett et al., 2018). Furthermore, the different strains show little evidence for clustering, which suggests that there were not multiple domestication events, but this might be due to extensive admixture amongst the progenitors of the different strains with the Wistar strain (Puckett et al., 2018). However, the rats being examined in these studies all derive from laboratory inbred strains, and it is unclear as to whether pet strains have been examined. The development of pet fancy rat breeds is unclear and rarely discussed in these papers. Although it might easily be assumed that pet strains derive from early laboratory breeding prior to the development of inbred strains, in fact the reverse is likely true and pet rats may harbor unknown diversity. The ancient Japanese strains of domestic rat have not been identified, nor have they been systematically looked for. This would suggest further research is required that incorporates rats bred for pet keeping and not just laboratory use.

Effects of Human-Associated Adaptation and Domestication

The nature of brown rat domestication presents an interesting case for tracking both the unintentional and intentional effects of domestication, but also likely human-induced adaptations that may have occurred prior to domestication. The effects of domestication on any one species, let alone one specifically bred for experimental use, are extremely wide ranging and cannot all be addressed here (for further review of differences between laboratory and wild rats, see Modlinska and Pisula, 2020), but some major elements will be outlined and described which are relevant to the concept of domestication more generally.

A number of studies identify differences in commensal brown rat populations that indicate that the animals from which domestic lineages derive had already undergone some degree of adaptation to human environments. This indicates that the different domestication events for brown rats probably occurred on populations with different levels of pre-adaptation to humans. Genetic analyses of the global commensal populations identify immune system genes as having been positively selected for in populations dispersed from their native range (Zeng et al., 2018). The conditions under which initial captive populations were kept prior to selective breeding will probably have exacerbated this, as ratcatcher accounts describe cages with capacities around 1000 and the individuals being "...piled up with rats, solid ... " (Mayhew, 1851: 19). The stock from which the domestic brown rat (in particularly within Europe) derives must thus have undergone 1) significant selective pressure and adaptations to commensal life histories, followed by 2) some likely adaptations to captivity, including to high population density and to rapidly changing environments (Hulme-Beaman et al., 2016). The "wild" state of the immediate ancestors of domesticate rats, then, probably reflected a certain amount of preadaptation to human environments and maybe even human proximity. This has been a particular issue with assessment of domestication experiments and the domestication syndrome, a suite of effects of domestication that are highly debated (Lord et al., 2020; Zeder, 2020). For example, the Russian farm fox experiment, where fur farm foxes were selectively bred for docility towards humans, has been held up as a model for domestication processes, but the animals had

previously been kept in non-natural environments (closed and tightly caged), presumably leading to a certain amount of prior adaptations to such conditions (Lord et al., 2020; but see Zeder, 2020). The extent to which domestication syndrome traits emerge or increase in prevalence in commensal or captive (but not domesticated) populations is very unclear, and lacks robust data (Lord et al., 2020; Zeder, 2020), but it is clear that some level of predomestication adaptations or shifts in allelic frequencies occurs in such populations (as seen with brown rats; Zeng et al., 2018).

Early studies have directly compared the physiology of wild commensal rats and domestic rats and found a number of changes. In domestic brown rats, one of the most obvious changes with domestication is the emergence of a wide array of coat colors—white, black, agouti, brown hooded, black hooded, and yellow (see Hedrich, 2019 for full list of strains and colors). Again one can note the early rat-catcher descriptions of different color morphs occurring, albeit rarely, in populations around London (Mayhew, 1851).

A number of organ size changes are also recorded with the adrenal glands, preputial glands, liver, heart, and brain all showing reductions in size (Richter, 1959; Kruska, 1988; Modlinska and Pisula, 2020). The changes in the brain regions in particular reflect reduction in size of brain regions that control motor function (Kruska, 1988). Changes are also present in the reproductive organs, with testes size in young males being larger in domestic rats, whereas testes size in commensal wild rats increases to eventually be larger in old males (Richter, 1959); this may indicate a shift in domestic animals toward sperm competition and rapid reproduction in younger males-a proposed result of domestication occurring in animals domesticated under conditions of higher population density (Hulme-Beaman et al., 2018). This also follows with observations that domestic rats are more gregarious than their wild counterparts (Figure 2C) and mate more readily (Galef et al., 2008). Domestic brown rats are noted as having numerous social and reproductive behavior traits not observed in wild strain colonies, including a heightened level of polyandry, group mating, and mate swapping during copulation (McClintock and Anisko, 1982; Schweinfurth, 2020). Behavior primarily differs between domestic and wild strain populations toward the introduction of unfamiliar rats (individuals that might be considered interlopers in a wild population) (Barnett and Stoddart, 1969; Boreman and Price, 1972). Laboratory strains of domestic brown rats will eventually accept interlopers (Barnett, 1960), whereas laboratory strains of wild brown rats will aggressively attack interlopers, regularly resulting in serious injury (Galef, 1970; Boreman and Price, 1972). These behavioral differences probably reflect the core of the domestication process, although domestication represents a huge range of traits and a continuum rather than an end point, behavioral changes, and the fixation of these in a population is central to the process.

Conclusions

Examining the pathways rats followed to domestication presents an interesting set of questions that are valuable to consider when trying to understand the concept of domestication and the overall process for other species. Firstly, in brown rats domestication is far more complex than it initially may seem, with multiple possible domestication events that appear to have elements from different pathways. The first, in Japan, appears to have followed a "directed pathway," but we cannot be sure of the status of their predecessors (i.e. wild, commensal or captive populations). The second and third, in Europe and North America respectively, stem from commensally translocated populations and may have even experienced some selective pressures similar to animals in the "prey pathway"-in which populations are managed prior to directed breeding selections-but under conditions of strict captivity and with subsets of individuals taken for different purposes and under the more clear "directed pathway." Each of these domestication processes is set against the clear backdrop of this species being highly commensal, and therefore might overall be considered part of the "commensal pathway" to domestication-a pathway which, after all, ordinarily implies eventual direct human intervention at later stages. Of particular relevance here is the fact that the modern domestic rat appears to be exclusively derived from populations that had already undergone commensal adaptations to high population density prior to domestication.

Although the laboratory rat might be the most commonly cited example of domestic brown rats; the rat did not jump straight from its commensal relationship to a laboratory domesticate via strict selective breeding, but rather via a number of intermediate stages for different purposes. The brown rat therefore demonstrates how different requirements of human societies may lead to domestication of the same species under different pathways and different selective processes. Overall, the surviving domestic rat populations of today appear to stem from a commensal/directed pathway; in contrast, had the 1800s rat-baiting colonies survived today the selective pressures involved might be considered close to those we would hypothesize to be associated with the prey pathway. Furthermore, it is not clear whether descendants of the domesticated Japanese Edo period rats still survive today, but they currently represent the earliest evidence for domestication of this species and a discrete domestication center in relation to later events in Europe and North America. The humble domestic brown rat therefore represents all the complexity of human influence on animals both across large geographic distances (different domestication events in different parts of the world) and through time (early domestication in Japan compared with later domestication in Europe and North American) and for different purposes (fancy rats, stock for blood sports and specific experimental breeds). In stark contrast to the enormous amount of knowledge we have of its biology, this review demonstrates we have limited knowledge of many aspects of its origins, with less certainty than is often assumed.

About the Authors



Ardern Hulme-Beamanis Leverhulme Early Career Fellow based in the Department of Archaeology, Classics and Egyptology at the University of Liverpool. He gained a BA in Archaeology and a MSc in Paleoecology from Durham University. Ardern received a joint PhD from the University of Aberdeen and the Muséum national d'histoire naturelle, Paris, where he studied the human-mediated dispersal of rats and the evolution of commensalism. He previously worked as a postdoctoral research associate on a large project investigating the origins of

dog domestication based across the Universities of Aberdeen, Liverpool and Oxford. Ardern primary research interests focus on the evolution and ecology of animals in association with humans. He has expertise in statistical shape analyses and virtual 3D reconstruction, which he applies to study the evolution of feeding and reproductive behavior in human-associated species. **Corresponding author**: ardernhb@gmail.com

David Orton is senior lecturer in zooarcheology in the Department of Archaeology at York, and a member of the BioArCh research group. He has a BA and PhD in archeology from the University of Cambridge and an MSc in zooarcheology from the University of York (a program that he now directs). Before returning to York, he held postdoctoral positions at SUNY Binghamton, Cambridge, and University College London. David works on animal remains from multiple periods and regions across (broadly) Europe, but is particularly interested in early farming



in the Neolithic of the Balkans and Anatolia on the one hand, and on animal evidence for urbanism and trade in medieval northern Europe on the other. The latter has involved working extensively on fishing and fish trade and most recently on the European history of black and brown rats.



Cucchi received its Thomas PhD from the Natural History Museum of Paris in 2005. He is a zooarcheologist whose research focuses on the origins, spread, and evolution of anthropogenic species over the last 15,000 yr. Using an integrated approach associating zooarcheological studies with the latest development in morphometric and molecular studies, he has published on animal domestication, commensalism, and dispersal in South Western Asia, China, Island South East Asia, and Europe. He is currently working on new methodological approaches of early process

of animal domestication in archeology, using functional plasticity in bone morphology and epigenetic markers.

Acknowledgments

We thank the Biodiversity Heritage Library for providing free access to numerous important early natural historical works touching on the brown rat, and Laura Koski for fruitful discussion of those works. We also thank Robert Lachlan for providing a photograph of social behavior of pet fancy rats. A.H.-B. was supported by the Leverhulme Trust (ECF-2017–315). D.O. was supported by the Wellcome Trust with a Wellcome Small Grant in Humanities and Social Science (20981/Z). We thank two anonymous reviewers for their extremely helpful comments and reviews.

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Perspectives

Fish domestication in aquaculture: 10 unanswered questions

Fabrice Teletchea

Unité de Recherche Animal and Fonctionnalités des Produits Animaux, Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement, Université de Lorraine, 54505 Vandœuvre-lès-Nancy, France

Implications

- Aquaculture is the fastest-growing food-production sector in the world.
- The number of farmed and domesticated fish species has increased tremendously in the past decades, even though the 20 most-produced species accounted for >80% of total fish aquaculture production.
- This article discusses 10 partially unanswered questions related to fish domestication that could help enhancing the sustainable development of aquaculture.
- Domestication is a powerful tool to continue improving the production of already domesticated species and farm new species, particularly those native, which could all be better adapted to cope with economic, social, and environmental issues.

Key words: diversification, fish domestication, selective breeding programs, sustainability, global issues

Introduction

The first trials of farming fish species for human consumption might date back to 8,000 yr ago, with the managed aquaculture of common carp (Cyprinus carpio) in Henan Province, China (Nakajima et al., 2019). Evidence of farming was also found on Egyptian tombs from about 3,500 yr, with some kind of control over the reproduction of Nile tilapia (Oreochromis niloticus) in irrigation ponds (Teletchea, 2019a). In Europe, the farming of common carp in ponds was already developed during the Middle Ages. The Italian "Vallicoltura" (extensive farming of various marine species in coastal lagoons and large open waterbodies) dates back to the 15th century. The French trout culture started around the second half of the nineteenth

doi: 10.1093/af/vfab012

century (Teletchea, 2019a). In North America, aquaculture started about 100 yr ago. In Africa, aquaculture dates back to the 1940s. In Australia, New Zealand, and diverse Pacific Island states, the development of aquaculture is even more recent. In conclusion, the rearing of fish is very old (Gjedrem et al., 2012), particularly in Asia (De Silva et al., 2009), even though this is not before the early 1980s that aquaculture truly boomed, becoming the fastest-growing food-production sector globally (Teletchea, 2016a; FAO, 2019). In only four decades, aquaculture production has surpassed capture fisheries, and today more than half of the fish destined to human consumption are farmed globally (Teletchea 2016a; FAO, 2019; Houston et al., 2020). The exponential growth of aquaculture has relied partly on the domestication of an increasing number of fish species (FAO, 2019; Teletchea, 2019b). The aim of the present article is to discuss briefly 10 partly unanswered questions linked to fish domestication, which could be taken into account to promote a more sustainable global aquaculture production.

Question 1: What Is Fish Domestication?

There is no scientific reason to consider fish domestication differently from any other animal domestication (Balon, 2004; Bilio, 2008; Hedgecock, 2012; Lorenzen et al., 2012; Teletchea, 2015a; Saraiva et al., 2019). Therefore, fish domestication could be defined as a dynamic and endless process, which starts as soon as individuals are transferred from wild to captive conditions (Teletchea, 2015a). Five genetic processes are involved in the evolution of fish during domestication: two uncontrolled (inbreeding, genetic drift), two partially controlled (natural selection in captivity, relaxation of natural selection in captivity), and one controlled (active selection) (Teletchea, 2015a). In addition, the diverse molecular mechanisms involved in 'nongenetic' modes of inheritance can alter aspects of genome activity and affect progeny gene expression (Adrian-Kalchhauser et al., 2020). Summing up, domestication allows adapting continuously a batch of fish to both captive conditions and humans, with the ultimate goal of modifying, generations after generations, selected traits, to produce, in most cases, more productive and efficient individuals (Bilio, 2008; Olesen et al., 2015; Houston et al., 2020).

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Question 2: What Is a Domesticated Fish?

For Balon (2004), animals become domesticated when they change form, function, color, and behaviour; often only partially resemble their wild ancestors; and survive poorly as feral forms if returned to the wild without human protection. For Bilio (2008), fish species are considered domesticated when they show first results of selective breeding or when no such evidence is found, after at least three successive cycles of reproduction (generations) under controlled conditions (the choice of three full cycles in captivity was an arbitrary criterion). Duarte et al. (2007) considered that fish are domesticated when breeding, caring, and feeding of organisms are controlled by humans. For Gjedrem et al. (2012), domesticated fish strains are the result of several generations of selection. Hence, rather than trying to define what a domesticated fish is, which could be in fine considered an arbitrary decision because it varies widely between authors and no clear threshold separates wild from domesticated animals (Teletchea, 2017), Teletchea and Fontaine (2014) coined a new concept (domestication levels) based on the degree of human control over the life cycle of farmed fish species. This domestication scale contains five levels (Table 1). According to this new classification, it was proposed that only fish species reaching at least the level 4 (full life cycle completed in captivity without wild inputs) could be considered domesticated. Yet, a domesticated fish is neither a definitive status as these animals continue evolving all the time (to cope with new captive conditions or because new traits are selected), nor a final end point of domestication because they can sometimes return to the wild, a process known as feralization (readaptation to the natural environment), which is one of the main issues of aquaculture globally (Lorenzen et al., 2012; Glover et al., 2017).

Question 3: How Many Fish Species Are Domesticated?

The number of fish species considered domesticated varies tremendously between authors from 2 for Balon (2004), 42 for Bilio (2008) to over 250 for Duarte et al. (2007). Yet, the number proposed by Balon (2004) is clearly too low because of his strict definition (see above). Conversely, the very high number documented by Duarte et al. (2007) simply reflects the growth of aquaculture globally (Hedgecock, 2012); farming a fish species does not necessarily imply that it has been domesticated (Bilio, 2008; Klinger et al., 2013; Teletchea and Fontaine,

2014). Among the 250 fish species listed by Duarte et al. (2007), which were established from the FAO database for the years 1950 to 2009, only one-third had reached the level 4 (n = 30) or level 5 (n = 45) (Teletchea and Fontaine, 2014); which is much closer to Bilio's estimations. Nearly a decade later, it is likely that new species have reached levels 4 and 5 (e.g., Teletchea, 2015b; Valladão et al., 2018) and probably 100 could be considered domesticated globally (see also FAO, 2019; Houston et al., 2020).

Question 4: How Long Does It Take to Domesticate a Fish Species?

Domesticating a fish species implies that the full life cycle is controlled in captivity without wild inputs (Table 1). The time required to reach this milestone varies tremendously between species, if ever attained (Bilio, 2008; Teletchea and Fontaine, 2014). Indeed, numerous farming trials of new species failed only after a few years mostly due to insufficient biological, ecological, and zootechnical knowledge (Teletchea and Fontaine, 2014). Key bottlenecks in closing the life cycle in captivity are (1) inadequate feeds, particularly for the first feeding of tiny larvae of numerous marine fish species, (2) poor gonadal development, and (3) lack of spawning (see also Bilio, 2008). Most often, we have no information about the domestication history of farmed species (Teletchea, 2019a); yet see for instance Gjedrem (2010, 2012) and Glover et al. (2017) for Atlantic salmon (Salmo salar) and Fontaine and Teletchea (2019) for Eurasian perch (Perca fluviatilis) (Figure 1A). In conclusion, domesticating a new fish species is a risky journey that may take years or even decades (Bilio, 2008; Teletchea and Fontaine, 2014; FAO, 2019).

Question 5: Is Fish Domestication Going too Fast?

Once the full life cycle is controlled in captivity, there are no longer exchanges between farmed individuals and their wild congeners, and domestication can proceed toward the production of improved individuals (Table 1). For some domesticated species, several generations under selection have allowed improving specific traits very rapidly (Olesen et al., 2015; Nguyen, 2016; Teletchea, 2016b; Houston et al., 2020). Therefore, the time lag between the onset of domestication and selective breeding can be considerably short

Table 1.	Description	of the	domestication	levels o	of fish	species	(modified	from	Teletchea,	2019b
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Level	Description	n _{species}	n _{families}	Three main families (<i>n</i>)
5	Selective breeding programs are applied focusing on specific goals	30	10	Cyprinidae (10), Salmonidae (8), Acipenseridae (5)
4	Full life cycle is controlled in captivity without the use of wild inputs	45	25	Cichlidae (6), Sparidae (5), Cyprinidae (4)
3	Full life cycle is controlled in captivity, yet wild inputs are still used	61	35	Sparidae (8), Cyprinidae (4), four families (3)
2	Only part of the life cycle is controlled in captivity due to key bottlenecks	75	39	Cyprinidae (9), Serranidae (5), Carangidae (4)
1	First trials of acclimatization to captive conditions	39	24	Cyprinidae (8), Sciaenidae (3), Siganidae (3)

n_{species}, total number of species per level; n_{families}, total number of families per level; n, number of species for the three main families.



Figure 1. Examples of two freshwater fish species that have reached in 2009 the level 4: European perch *Perca fluviatilis* (A) and the level 5: common carp *Cyprinus carpio* (B). Pictures taken from www.storefish.fr (Teletchea and Teletchea, 2020).

in aquaculture (less than a decade), with both occurring in tandem in many cases (Houston et al., 2020). However, it was found that without proper management, numerous breeding programs resulted also in a quick loss of genetic diversity because of inbreeding, possibly leading to a decline of productivity, a reduced population fitness, and an increased susceptibility to stress and disease (Olesen et al., 2015; Nguyen, 2016; Houston et al., 2020). Therefore, caution should be taken not to go too quickly when implementing breeding programs and adequately balance market (e.g., growth rate, fillet quality) and non-market values, such as ethics and welfare (Saraiva et al., 2019). Research has pushed the physiological limits of many fish species in growth, fertility, and size, as a consequence of (or resulting in) highly artificial conditions, possibly altering their welfare, which is one of the key issues of aquaculture today (Saraiva et al., 2019). It is also crucial to maintain sufficient genetic variability (e.g., establish a base population with ample genetic variability, keep a large effective population size, and introduce genetic variability from outside the breeding stock) of domesticated and selected fish to ensure that they are more robust and able to cope with various environmental changes (Olesen et al., 2015; Nguyen, 2016; Teletchea, 2016b). Supported by continuous advances in sequencing and bioinformatics, genomic tools appear now hugely valuable to inform sustainable genetic improvement and their affordability and accessibility mean that they can now be applied across the broad range of aquaculture species and at all stages of the domestication process to optimize selective breeding (Houston et al., 2020).

Question 6: What Are the Most Domesticated Fish Species?

Thirty species belonging to 10 families have reached the level 5 (Table 1), including Acipenseridae (n = 5), Cichlidae (n=1), Cyprinidae (n = 10), Gadidae (n = 1), Ictaluridae (n = 1), Moronidae (n = 1), Paralichthyidae (n = 1), Salmonidae (n = 8), Scophthalmidae (n = 1), and Sparidae (n = 1) (Teletchea, 2019b). Among those 30 fish species, common carp (Figure 1B) and Nile tilapia are probably the most selected for the longest period of time globally (Bilio, 2008; Gjedrem et al., 2012; Nguyen, 2016; Teletchea, 2019a). In Europe, the most domesticated and selected species are common carp, rainbow trout (*Oncorynchus mykiss*), Atlantic salmon, gilthead sea bream

(Sparus aurata), European seabass (Dicentrarchus labrax), and turbot (Psetta maxima) (Janssen et al., 2017).

Question 7: Which Traits Were Selected?

Selective breeding programs in fish have historically focused on improving growth (Nguyen, 2016; Gjedrem and Rye, 2018). Genetic gain averages about 10% to 20% per generation for growth rate when this is the main, or only, selected trait (Gjedrem et al., 2012). In addition to growth, feed conversion efficiency, age at sexual maturity, improved resistance to bacterial and viral diseases, and a number of traits related to product quality (e.g., muscle lipid content, flesh color, tenderness, flavor) have been gradually included in various breeding programs, particularly for Atlantic salmon (Gjedrem, 2010, 2012). In a recent survey conducted among breeding companies of five species farmed in Europe, Janssen et al. (2017) found that growth performance was universally selected upon. Among the 27 breeding programmes, both morphology and disease resistance were included in 15, product quality in 13, processing yield in 12, and reproduction and feed efficiency in 7 (Janssen et al., 2017). In conclusion, the future seed market will most likely continue to request genetic material that is selected for growth rates as well as other traits (Olesen et al., 2015; see also Table 25 in FAO, 2019).

Question 8: Is there a link between fish domestication level and production volume?

It is impossible today to definitively conclude whether domestication levels (Table 1) and production volumes are positively linked given the actual nature of data provided to the FAO by its members and associated nations (Klinger et al., 2013; Teletchea and Fontaine, 2013). Yet, Bilio (2008) highlighted that the percentage of domesticated species is increasing with the production level. The share of domesticated species is probably close to zero as long as the production per species remains below 100 tons and close to 100% for species reaching a production of 1 million tons (see Table 7 in Bilio, 2008). In other words, fully closing the life cycle in captivity seems positively related to a significant production: the top 15 most-produced species in 2009 all have reached level 4 or 5 (Teletchea and Fontaine, 2013). This includes species for which the onset of domestication is either centuries old, such as common carp or Nile tilapia, or a few decades old, such

as Atlantic salmon (Teletchea, 2019b). In Europe, the proportion of aquaculture production that originates from selective breeding is very high, with a market share that exceeds 80% (Janssen et al., 2017). Atlantic salmon clearly appears as an outlier with close to 100% of the production that are now based on improved stocks (Gjedrem, 2010; Gjedrem et al., 2012). Yet, for most farmed species reaching level 4 or 5 does not necessarily imply that their total aquaculture production is based on this level (stocks of the same species can be at different domestication levels). Overall, only 10% of the global aquaculture production comes from genetically improved stocks (Gjedrem et al., 2012; Olesen et al., 2015).

Question 9: Should We Stop Domesticating New Fish Species?

The boom of fish aquaculture has relied partly on the domestication of an increasing number of fish species, even though most domestication experiments stopped or failed to reach a significant volume and the global production is today heavily skewed toward the farming of a few species (FAO, 2019; Teletchea 2019b; Sicuro, 2021). The 20 most-produced species account for >84% of total production (FAO, 2019; Teletchea, 2019b). The main farmed species have been extensively introduced around the world (De Silva et al., 2009; Teletchea, 2019a). Seven of the eight most widely farmed fish species are more frequently reported by countries where they are nonnative than by countries where that are native (FAO, 2019). For instance, common carp is farmed in 48 countries, among which 37 where it was introduced (FAO, 2019). Likewise, Nile tilapia is farmed in 45 countries (33 introduced) and rainbow trout in 45 countries (40 introduced) (FAO, 2019). The introduction of non-native species can affect biodiversity, directly or indirectly, and these impacts can be immediate or long term (De Silva et al., 2009). Therefore, reducing the dependence on non-native species, and thereby minimizing possible negative impacts on biodiversity, is increasingly perceived as an imperative for the sustainable development of aquaculture (De Silva et al., 2009). In this context, there are conflicting demands for further diversification versus the need to focus and improve the efficiency of production of existing farmed species (FAO, 2019). Bilio (2008) considered that it is no longer desirable to seek further diversification by subjecting yet more species to experimentation, but rather restrict our efforts to a few species and exploit intraspecific diversity potential, that is, the still largely unknown genetic diversity resources within truly domesticated species. Conversely, there is still huge potential for domesticating new fish species, particularly native ones, to develop a more diverse aquaculture sector likely to be more resilient to challenges of environmental change (Valladão et al., 2018; FAO, 2019; Fontaine and Teletchea, 2019). Such a strategy might also help to eliminate, or at least minimize, the adverse ecological and genetic impacts of either direct or indirect introduction of non-native species (De Silva et al., 2009). In recent years, the willingness to promote native species for aquaculture enterprise has resulted in significant changes in various countries,

particularly in South America (Valladão et al., 2018). For example, the production of pacu *Piaractus mesopotamicus* has increased significantly in recent years, exceeding the production of the non-native rainbow trout in 2012 in Argentina (Valladão et al., 2018). The contribution of native species to global aquaculture will perhaps increase, resulting in a more diversified and even production than today (Teletchea, 2019b). In conclusion, it is likely that both intra- and interspecific diversification will be pursued at least in the coming decade, that is to continue improving already domesticated and selected species and to farm new fish species (FAO, 2019; Teletchea, 2019b).

Question 10: Do We Already Need a Sixth Level of Domestication?

Given the tremendous progresses in fish domestication, it might be timely to propose a sixth level of domestication for the species for which selection has resulted in strains. According to the FAO (2019), a strain is a "farmed type of aquatic species having homogeneous appearance (phenotype), homogeneous behaviour and/or other characteristics that distinguish it from other organisms of the same species and that can be maintained by propagation." Some strains (notably for common carp and rainbow trout) are already officially registered in a limited number of countries (Bilio, 2008), but there are still very few distinct, stable, and reproducible strains in aquaculture (Bilio, 2008; FAO, 2019). One very well-known example is the genetically improved farmed tilapia (GIFT) strain developed in the early 1990s from a base population including wild and farmed strains from eight African and Asian countries (Gjedrem, 2012; Nguyen, 2016; Houston et al., 2020). The GIFT strain is now farmed in 16 countries across Asia, Africa, and Latin America and grows 85% faster than the base population (Houston et al., 2020). Similarly, the Atlantic salmon is certainly the fish for which the domestication history is best known (Teletchea, 2019b) and was the first species to be subject to a systematic family-based breeding program (Gjedrem, 2010, 2012). Currently, over 12 generations have been consecutively bred in captivity for the oldest breeding programs in Norway and multiple strains were established in several countries (Glover et al., 2017). Nevertheless, it might still be too early to propose a sixth level of domestication for only a few strains in a handful of species; this situation might change quickly, and many recognizable strains could be soon officially recognized and registered as observed for the thousands breeds in farmed land mammals and birds (FAO, 2019).

Conclusions

Domestication is a long and endless process that allows adapting fish to both captive conditions and humans. This process started only a few decades (or even years) ago for most farmed species, and therefore probably less than one-third could be considered domesticated. Several traits, among which growth, were modified during domestication. New breeding programs will need to balance market and non-market values

About the Authors



Fabrice Teletchea studied marine biology and then systematics in France. Since 2010, he is associate professor at the University of Lorraine in Nancy, France. He first worked on fish taxonomy and then moved to the study of fish domestication in aquaculture. He developed a comparative framework of the reproductive strategies of European freshwater fish species in order to better understand the different trade-offs observed at the earlylife stages (www.storefish.org), to help domesticating them more efficiently. Besides his research and teaching activities,

he is in charge of a professional bachelor entitled "Inland Aquaculture and Aquariology" for nearly 10 years at the IUT Nancy-Brabois. **Corresponding author:** fabrice.teletchea@univ-lorraine.fr

while maintaining a sufficient genetic variability to ensure that fish are productive as well as robust enough to cope with various environmental changes. The sustainable future of aquaculture will rely first on the continuous improvement of already domesticated fish species and second on our willingness and capacity to diversify the number of farmed, preferably native, species to promote a more diversified and even aquaculture production.

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Perspectives

Waterscapes domestication: an alternative approach for interactions among humans, animals, and aquatic environments in Amazonia across time

Gabriela Prestes-Carneiro,[†] Roberta Sá Leitão Barboza,[‡] Myrian Sá Leitão Barboza,[†] Claide de Paula Moraes,[†] and Philippe Béarez^{||}

[†]Anthropology and Archaeology Program, Institute of Social Sciences, Federal University of Western Para (UFOPA), Santarém, Pará, Brazil [‡]Laboratory of Teaching, Research and Fisheries Extension for Amazonian Communities (LABPEXCA), Institute of Coastal Studies (IECOS), Federal University of Pará (UFPA), Bragança, Pará, Brazil

^{II}Archéozoologie, archéobotanique: sociétés, pratiques et environnements (AASPE, UMR 7209), CNRS, Muséum national d'histoire naturelle, Paris, France

Implications

- In this article, we propose the "waterscape domestication" concept as a way to understand how humans and animals have interacted throughout history in the many aquatic environments in Amazonia.
- To support our proposal, we present and discuss historical and contemporary cases of interactions between forest people and animals in waterscapes. We describe archaeological structures and management practices of ponds, dams, and turtle and fish corrals.
- Through archaeological, ethnohistorical, ethnoecological and ethnographic studies we show the domestication concept should be broadened to include the worldview of forest people and their interactions with Amazonian waterscapes.

Key words: Amazonia, animal domestication, archaeology, water technologies, waterscape

Introduction

Animal management and domestication have been widely interpreted and studied in relation to terrestrial mammals; however, there are still debates over what "domestication" means for aquatic animals. Fishing has deep archaeological roots, as early as

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doi: 10.1093/af/vfab019

the Paleolithic (e.g., Cleyet-Merle, 1990; Braun et al., 2010; Fujita et al., 2016). There is solid evidence that specialized fish production and management began around 3500 BC in freshwater systems in China (Malindine, 2019), but there is less solid evidence that it may have begun in the same country as early as 6000 BC (Nakajima et al., 2019). Egyptian tomb art suggests management of the Nile tilapia (*Oreochromis niloticus*) around 1500 BC (Harache, 2002). In Europe, the common carp (*Cyprinus carpio*) was farmed by the Romans about 2,000 years ago but was not domesticated until medieval times (Balon, 2004).

Forest people have interacted with and managed aquatic and terrestrial environments across time in Amazonia, vet, compared with the Middle East and European centers of faunal domestication, few animals in Lowland South America, specifically Amazonia, have been domesticated. The term "forest people," as many of the traditional people in Latin America recognize themselves, is not used here in the literal sense since it does not only refer to people who inhabit forested environments, but it also refers to multiple collectives and human groups that commonly held lands and natural resources; Allegretti, 1989; Almeida, 2008. In this way, this term encompasses traditional people from rainforest, dry forest, and palm forest, liana forest, savanna, wetland, and several others. In the Andes, the classic examples of domestication are the llama (Lama glama), alpaca (Vicugna pacos), and guinea pig (Cavia porcellus) (Stahl, 2008). As defined by the naturalist Wallace (1858), the traditional concept of domestication is related to human supremacy in the control of nonhuman species (Barboza, 2019). For biologists, the domestication process generally implies modification of a species' genetic heritage. This develops a novel set of morphological features known as the "domestication syndrome" (Harlan, 1992). The only case of classical animal domestication that could have taken place in the tropical lowlands of South America during the same period is that of the Muscovy duck (Cairina moschata) (Stahl, 2005).

Although classical animal domestication (Stépanoff and Vigne, 2018) was lacking in the Amazon, many wild species have been kept as pets (in pet-keeping relationships, wild animals are captured and adopted but they are neither breed nor consumed by local people; Erikson, 2012), and recent studies suggest that human groups significantly altered Amazonian landscapes. A possible factor of animal non-domestication in the lowlands is how indigenous Amazonians interact with animals (Stahl, 2014). Inspired by Viveiros de Castro (1998) and Descola (1986, 2013), Stahl (2014) postulates that indigenous people eschewed subjugating animals to a position of dependence and subordination. Several of altered landscapes may be related to structures designed to keep aquatic animals in captivity or to "enhance the natural habitats of wild fish to increase their availability" (Erickson, 2008, p. 174). This seems to be the case of pre-Columbian and modern structures (i.e., ponds, corrals, dams, artificial wetlands, raised field canals, causeways, and other water management techniques) associated with fish and water management (Erickson, 2000, 2008; Lombardo and Prümers, 2010; Blatrix et al., 2018).

Studies have highlighted the importance of the domestication process in Amazonia, but most of them are restricted to populations of terrestrial plants and animals (Viveiros de Castro, 1998). An exception is Sautchuk (2007), who calls attention to relationships among humans and aquatic animals, mainly fish. Therefore, we aim to broaden domestication concepts based on the evidence of physical structures that demonstrate interactions between humans and waterscapes in Amazonia.

It should be recognized that the relationship between indigenous people and aquatic environments, albeit not specifically in relation to domestication, was earlier documented in the literature (Steward, 1948; Sauer, 1952); however, the idea of waterscape domestication is nonetheless under-emphasized. To support our proposal, we first provide a brief conceptual background for the concept of waterscape domestication, and, second, we provide a repertoire of historical and recent cases of interaction of forest people with animals in waterscapes, describing archaeological structures and management practices. Finally, we discuss how aquatic environments and their constituents-animals and water-have been modified through interaction with humans. We also consider that humans can be modified in these interactions, but it is not our intention to enter into a more detailed discussion of this aspect in the present text.

Amazonian Hydrology

Amazonia is the region that is drained by the Amazon River and its tributaries together with adjacent lowlands (Balée, 2003). The Amazon region is not uniform but is composed of different environments, such as floodplains, upland forests, savannas or (*llanos*), and mangroves, each of which has its particularities (Moran, 1990). Floodplains (also known as *várzeas*) are low-relief areas near large rivers, which are periodically flooded. Floodings are due to the lateral overflow of rivers or lakes and by the rain or groundwaterflood pulse (Junk et al., 1989). Generally, there is a 6-month rainy season where plains are flooded, however they can remain inundated for the majority of the year. Floodplains are environments of high biological productivity due to the large amount of suspended material carried by the Amazon River and the presence of floating aquatic plants (Sioli, 1984). Upland forests (or terra firme) are the highest areas of the Amazon and are not flooded. The Amazonian savannasknown as cerrado in Brazil, and Llanos in Colombia and Venezuela-are mainly situated in the boundaries of the Amazon region. They have a hyper-seasonal regime, with a strong dry season and a strong wet season, which creates extensive areas of flooded savanna. The llanos generally have poor drainage of the soil, which causes water to stagnate for months (Moran, 1990). Mangroves are marginal and unique ecosystems, defined by daily tide variations and sea (salt water) influence (Vannucci, 2001). Each one of these environments has a different relation with water, even in noninundated landscapes such as the upland forests has aquatic landscapes such as streams. All the environments change every year, with the arrival of the rainy season. The volume of water, the speed at which it arrives, and the elements that it brings (animals, plants, nutrients, and salinity) shape and modify the landscapes. The observation of these dynamics is crucial to understand human-made water structures and, therefore, the structures described below need to be understood based on the environmental context in which they are embedded.

Conceptual Background for Waterscape Domestication

Waterscape concepts gained theoretical shape and became widely used from the work of Swyngedouw (1999). As an aspect of political ecology, Swyngedouw (1999) uses the term "waterscapes" to emphasize the hybrid character of the aquatic landscape and to highlight that nature and society are deeply intertwined. Swyngedouw (1999) investigates the water politics and engineering in Spain's modernization process and shows that Spanish waterscapes and societies embody a multiplicity of historical–geographical relations and process. According to him, social interactions and power relations coproduce waterscapes.

Inspired by Swyngedouw's conceptualization of waterscapes, various and complementary conceptual framings have been used. Some of them encompass local cosmologies, knowledge, and identity, as well as the connection between the land, water, humans, and nonhuman beings. Strang (2005), for instance, argues the importance of sensory, aesthetic, and imaginative dynamics in people–water interactions, fundamental for the constitution of social identity. She demonstrated that the cultural meaning of water—or "fluidscapes" as she prefers to call— among Aboriginal societies in Australia—is intimately related to identity construction. Here, we adopt the concept of waterscapes based on its meaning and value, and in recognition of forest people ontology and encounters among multiple beings, as stressed by Gagné and Rasmussen (2016, p. 138):

In short, the concept of waterscape, as it has been developed at the crossroads between political ecology and studies of science, is useful for grasping how places are produced in uneven encounters and how water distribution and equity (or lack thereof) are fundamental features of these encounters. Furthermore, the concept leads us to further nuance these questions by examining a variety of ways of knowing and interacting with water in different waterscapes.

Additionally, Gagné and Rasmussen (2016) highlight the boundaries and interfaces between water and land based on "amphibious anthropology" framework. Societies involved in these landscapes are nurtured and disrupted by the changing flow of water (Gagné and Rasmussen, 2016). It is important to recognize the confluence of land and water and the influence of the flow of water in these landscapes. Short-term fluctuations and seasonal variations provoked by water movements—either by rainy season or by the influence of the moon—are crucial elements in waterscape dynamics in which humans are engaged.

Previous literature on domestication, especially anthropological and historical ecology studies (Teletchea and Fontaine, 2012; Tsing, 2012), has criticized the traditional discourse on domestication that assumed the notion of human control over a passive nature (Smith, 1995). Besides this, researchers complain about the intrinsic idea of a defined frontier between "wild" and "domesticated" species (Levi-Strauss, 1952). Based on these epistemological problems in the domestication discourse, scholars working in Amazonia recommend replacing the domestication, familiarizing predation, co-domestication, mutual-domestication, and several others (Morim de Lima, 2017; Fausto and Neves, 2018; Carneiro da Cunha, 2019). However, none of them debate the cases of human interaction with aquatic animals and environments.

In relation to "domestication of water," archaeologists Mithen (2010) and Garfinkel et al. (2006) refer to this concept by arguing that the development of water management in Late Neolithic populations fostered the emergence of ancient cities in Jordan Valley. They found archaeological remains of cisterns, wells, dams, aqueducts, a system of extensive series of structures for plant irrigation, and various water supply management structures in several parts of Jordan. This notion considers humans as the main manipulator and transforming agent of the natural properties of water for his own needs (Mithen, 2010).

Although the original meaning of domestication may have a connotation of "domination," Macauley (2005) addresses that domestication has another interpretation and contributes to better understanding of our relations with technology and the aquatic environment. According to Macauley (2005, p. 168), "water also carries and conducts values to us" and "domestication is also cognate with *domus* (house or home), thus rendering something very particular—in this case water known and relatively familiar on an everyday basis."

In the present paper, we prefer to readapt the "domesticated landscape" concept and we propose the term "waterscape domestication" to describe the interactions among humans, other beings (here, we refer to beings of multiple natures and morphologies—plants, stones, and spirits; Viveiros de Castro, 1998), and waterscapes in the Amazon and to extend the notion of "domesticated landscape" to aquatic environments. The "domesticated landscape" was first defined by Yen (1989) and Clement (1999,pp. 191–192), and Erickson (2008, p. 158) reviewed the concept. According to Erickson (2008, p. 158):

Domestication of landscape implies all intentional and nonintentional practices and activities of humans that transform the environment into a productive landscape for humans and other species. Domesticated landscapes are the result of careful resource creation and management with implications for the diversity, distribution, and availability of species. Through their long-term historical transformation of the environment involving transplanting of plants and animals, selective culling of non-economic species and encouragement of useful species, burning, settlement, farming, agroforestry (forest management), and other activities discussed in this paper, humans created what we recognize and appreciate as nature in Amazonia. Through the perspective of historical ecology, however, we see that nature in Amazonia more closely resembles a garden than a pristine, natural wilderness. Rather than "adapt to" or be "limited by" the Amazonian environment, humans created, transformed, and managed cultural or anthropogenic (humanmade) landscapes that suited their purposes. The cultural or anthropogenic landscapes range from the subtle (often confused with "natural" or "pristine") to completely engineered.

Clement and Cassino (2018) indicates that Amazonia, as well as all continents with human societies, has a mosaic of landscapes with different degrees of domestication. A sequence of categories of landscapes was classified by Clement and Cassino (2018) according to the intensity of landscape intervention and manipulation. A detailed classification of the degrees of intervention in waterscapes, in the parameters proposed by Clement (1999) for landscape, is an important work to come. However, for now, we suggest that different interventions can be perceived in terms of the longevity and durability of their brands in the environment.

In addition to terrestrial management, Erickson (2008) also included water management (river cutoffs, transportation and communication networks, and water control) and fisheries management as elements of a domesticated landscape. Considering this proposition and drawing from reflections about waterscapes interactions and complexity, we examine how waterscapes and their constituents have been managed as a complex and integrated system. The notion of waterscapes should not always be associated with the idea that water is abundant, as there are many relatively dry interfluvial areas in

Amazonia. What we emphasize here is that indigenous peoples managed the waterscapes using the water when it was available. The concept also considers the longitudinal dimension of rivers, with water movements (flooding, broadening of streams, and receding waters events) and fish migrations.

Archaeological and Historical Evidence of Managed Structures

Unlike most of the domesticated mammals, such as pigs or cattle, fish raised in ponds do not appear to have undergone morphological changes in their anatomy. Thus, the evidence of "confinement" is noticeable mainly in archaeological land-scapes and ethnohistorical and ethnographic accounts (Figure 1). In the Amazon Basin, there is a dearth of archaeological research concerning what structures are connected to fishing and water storage and what their function may have been. This contrasts with the information available on the Brazilian Atlantic coast (Nery, 1995), the Amazon River estuary (Bezerra, 2017), Atlantic coast of southeastern and southern Brazil (Noelli et al., 1995; Borges, 2016), Pacific Coast (Favier Dubois et al., 2019), and the Andes (Lane, 2014).

Artificial ponds

The first mentions of artificial ponds in the Amazon appear in the reports of the first Europeans to navigate along the Amazon River. Friar Gaspar de Carvajal mentions the abundance of fish, turtles, manatees, and birds found in the villages they passed. At one point, he mentions "[...] there was great food, there were turtles in corrals and water huts, meat, and fish and bizcocho, and they were in such abundance that a total of a thousand men could eat for a year [...] "(Carvajal, [1542] 1942, p. 27). However, from an archaeological and ethnographic point of view, these structures are still little known. In numerical terms, the Bolivian Amazon region is, until now, the place with the largest number of artificial ponds. In the Baures region, between the Guaporé and Mamoré rivers, more than 382 ponds have been recorded (Blatrix et al., 2018). Southeast of the Baures region, Prümers (2007) identified a set of artificial ponds near monumental platforms (lomas) in the Llanos de Mojos region, Bolivia. The ponds found at the Loma Salvatierra archaeological site are approximately 30 m wide and 2 m deep (See Figure 1(5)). A core sample from one of the ponds was taken and a layer of clay loam, rich in organic matter, was interpreted to be the bottom of the pond and delivered calibrated radiocarbon dates between AD 1000 and AD 1200 (Lombardo and Prümers, 2010).

The archaeological fish fauna from the Loma Salvatierra site is composed mainly of small-sized fishes, including undetermined small sardines (Characidae), *pirañas* (Serrasalmidae) and *serepapas* (Cichlidae), swamp-eels (*Synbranchus* spp.), and lungfishes (*Lepidosiren paradoxa*). These species are quite resistant to aquatic environments with low oxygen conditions and are often found in modern artificial ponds in the region. These facts suggest that the function of these structures was to store water and fish (Prestes-Carneiro et al., 2019). In the Llanos de Mojos region, there are ponds associated with raised fields in the Exaltación region (Iriarte and Dickau, 2012; Rodrigues et al., 2017); however, they have been neither dated nor studied (see Figure 1(3)). Nowadays, such ponds, both ancient and modern, are exploited by local women who use cotton fishing nets to capture available aquatic species (see Figure 2).

In the Central Amazon, there are several natural lakes that are seasonally affected by the alternating flood dynamics in the basins of the Negro and Amazon rivers. Several archaeological sites are strategically located near these lakes. In Lago do Limão (Moraes, 2006, 2013), this dynamic can radically transform the landscape, sometimes supplying the lake with black waters from the Negro river (most of the year) or with muddy waters from the Amazon river. In addition, controlling the periods of extreme flow in the lake system is a guarantee of abundant fishing. Digging or reestablishing channels to access parts of the system that are becoming disconnected is a task still performed by the populations living in the region. In the lake areas, it is still common that for a few days at the end of the low-water season, fishermen from traditional communities gather in large numbers for the "days of the fish with their heads out" (Moraes, 2006).

This current dynamic makes it difficult to identify which of these structures may be related to the same period of the archaeological sites, since structures managed today may only be the continuity of management. In any case, Schmidt et al. (2014) suggest that some excavated ponds documented in the floodplains near the Laguinho site (Central Amazon) may be associated with the occupation of the site.

Artificial ponds are found in the Belterra Plateau (~2,000 km²). Of the 68 recorded archaeological sites, 35 have artificial or natural ponds principally located near streams, yet far from large rivers (Stenborg, 2016). However, the only pond systematically excavated by researchers was located near the Cedro site (see Figure 1(6)). The pond is approximately 1.1 m deep and 12 m wide. On the banks of this pond, clay balls were found that seemed to have served as support for the walls of the pond (Troufflard and Travassos, 2019). The Cedro site, like most of the sites on the Belterra Plateau, is dated between AD 1300 and AD 1400 (Nimuendajú, 1952; Stenborg et al., 2018; Troufflard and Travassos, 2019). In the ponds of Belterra, no faunal remains were preserved and there was no zooarchaeological investigation.

In the lower Madeira river, at the Guajará archaeological site, Moraes (2013) mapped an oval hollow, 38×32 m in size, 2.5 m in deep, with a flat bottom formed by excavation and the heightening of the banks with removed soil to form a 1-m berm (see Figure 1(7)). Recovered materials are associated with the polychrome tradition, dating to around AD 1000. The structure in question is not yet dated. In the upper Xingú region, Heckenberger et al. (2003, p. 1711) mentioned several "wetland features, such as bridges, artificial river obstructions and ponds, raised causeways, canals, and other structures, many of which



Figure 1. (a) Map showing the distribution of water management systems in the archaeological and historical record. The ecosystem in which the structure is placed follows in parenthesis. (b) Images of the structures (1) Water retention systems from the Apere savannas in the Venezuelan Llanos: ~AD 500 to AD 1400 (Zucchi, 1984) (savannas). (2) Archaeologically observed artificial ponds in Lago do Limão site, in the central Brazilian Amazon interpreted as turtle corrals: ~AD 300 to AD 1200 (Moraes, 2006) (floodplain). (3) Archaeological ponds associated with raised fields in the Exaltacion área, Bolivia: ~AD 400 to AD 1400 (Rodrigues et al., 2017) (savanna). (4) Archaeological earthen fish weirs associated with ponds in Baures, Bolivia: ~AD 1000 to AD 1300 (Erickson, 2000; Blatrix et al., 2018) (savanna). (5) Archaeological ponds nearby earthen platform sites (Lomas) in Trinidad, Bolivia: ~AD 1000 to AD 1200 (Lombardo and Prümers, 2010; Prestes-Carneiro et al., 2019) (savanna). (6) Thirty-five archaeological ponds recorded on the Belterra Plateau, Brazil: ~AD 1300 to AD 1400 (Nimuendajú, 1952; Stenborg et al., 2018; Troufflard and Travassos, 2019) (uplands). (7) An archaeological pond at the Guajará site near Borba, Brazil: ~AD 1000 (Moraes, 2013) (floodplain). (8) Turtle corrals that were used by the Conibo in the Ucayali, Peru: 19th century (Marcoy, 1875) (unknown). (9) Archaeological pond associated with raised field in the San Borja área, Bolivia; no data available (Iriarte and Dickau, 2012) (savanna). (10) River dams observed by Nimuendajú (2004) between AD 1922 and AD 1924 reported in Rio Preto do Pantaleão in the region of Autazes, Brazil (unknown). (11) Seasonally flooded, dug depressions associated with archaeological occupations of raised platforms, or *Tesos*, on the Marajó Island, Brazil: ~AD 500 to AD 700 (Schaan, 2008; Schaan et al., 2010) (mangrove). (12) Artificial obstructions of river courses and ponds, possibly related to fishing, in the área of the Upper Xingú River, Brazil: ~AD 1200 to prese

are still in use today." Ponds located in Central Amazonia, Belterra plateau, and Lower Madeira River have well-defined circular and oval shapes. Additionally, there are also ponds resulting from the construction of other structures (i.e., mounds, raised fields, and terraces).

In such cases, aquatic animal breeding or exploitation may have occurred, because the conditions created were favorable to their survival. Examples include the crater-type depressions next to the artificial mounds, such as at the Teso dos Bichos site, on Marajó Island, dated to roughly AD 500. At this site, Schaan (2008, p. 344) postulated that these depressions at this site were used as "fishponds" to hold fish at the beginning of the dry season. Fishing in these places is still practiced today on Marajó Island. Similar crater-type depressions in southwestern Amazonia may have served an analogous purpose (Erickson and Balée 2006). Other examples of ponds and reservoirs are found in the Andes. Locally known as *q'ochas*, they are important for controlling water and seasonal runoff and are used as either drinking ponds or reservoirs for animals (Lane, 2014).

Turtle corrals

Corrals are geometric structures surrounded by wood sticks, vertically arranged, forming an enclosure fence for live Giant South American River Turtles (Podocnemis expansa). Usually, female turtles captured in the dry season on beaches during their breeding period were stored in corrals for later consumption (Marcoy, 1875; Goeldi, 1906; Bates, 1944; Veríssimo, 1970; see Figure 1(8)). These enclosures have been described as natural or artificial lakes located in domestic backyards (Ferreira, 1903) that were used by Amerindian communities since the 15th century to conserve rainwater (Acuña 1994 [1641]). Almost all reports describing Amazonia by chroniclers and naturalists between the 16th and 17th centuries note that corrals were commonly used to store live animals (Machado, 2016: 60). In the 18th century, corrals provided the main food for the local population as well as for soldiers and the Portuguese settlers (Ferreira, 1903). Because of their great relevance in the local diet, these turtles were known by the local population as "bois do rio," "river bulls" (Moll and Moll, 2004), or "Amazonian bull" (Veríssimo, 1970 [1875], Gilmore, 1997) considering the great amount of meat that they provided.

Turtles were an economically safe species providing a highly reliable source of food (Ferreira, 1903, p. 184). They could be kept in these enclosures for up to 6 months (Daniel, 2004 [1741–1757]) without the need for food and slaughtered as needed (Santos and Fiori, 2020, p. 357). In the Upper Amazon, turtles could be kept for years and they even reproduced in confinement. According to Silva-Coutinho (1868): "In the Upper Amazon an excavation is practiced in the garden which is filled with water, the turtles live there perfectly well for several years,

lay eggs at the suitable time and reproduce with the greatest ease." Although recent efforts have been undertaken to breed turtles in the Amazon, specific questions need to be addressed to better understand the return on investment of keeping turtles in the past in comparison to other species. Were they fed in corrals, and if so, with what? Contemporary studies show that *P. expansa* is herbivorous in the wild (Pritchard and Trebbau, 1984) and omnivorous in captivity (Malvasio et al., 2003). According to historical accounts, turtles kept in corrals were fed with tree branches, leaves of plants such as *aninga* (*Montrichardia linifera*), vegetables, and manioc flour (Acuña, 1994 [1641]; Silva-Coutinho, 1868; Vieira, 1970).

Despite ethnohistorical reports, from an archaeological point of view, it is difficult to say definitely that excavated structures found in Amazonia were specifically built for turtle corrals. Moraes (2006) excavated one (12×6 m and 1.2 m in depth) of the three ponds recorded at the Lago do Limão site (Central Amazonia), revealing stake marks on the edges of a trench opened by researchers, similar to ethnohistorical descriptions of turtle corrals (see Figure 1(2)). While radiometric dates remain to be validated, the time of construction of this particular structure is estimated to be between AD 300 and AD 1200. At the nearby, contemporaneous Hatahara site, zooarchaeological turtle remains were found. The subsequent analysis of this material showed that the remains were of individuals of the genus Podocnemis with an estimated length between 30 and 70 cm. This suggests a conscious prey selection guided by both the choice of taxon and the size of the individuals (Prestes-Carneiro et al., 2016).

Because Brazilian legislation prohibits capture and consumption of chelonians, except in very peculiar cases (1998), corrals are rare today. However, in the Jau river (Central Amazonia), some local villages maintain other species of chelonians (*Podocnemis erythrocephala, Peltocephalus dumerilianus*, and *Podocnemis unifilis*) for many months in corrals next to their residences (Pezzuti et al., 2004). It is also important to point out the existence of another type of corral, known as beach corral. This refers to a trap used on the beach edge for the capture of *P. unifilis* females in the Jaú river (Pezzuti et al., 2004; Rebêlo et al., 2005).

Fish weirs

Here, we use "fish weir" to designate an obstruction placed in tidal waters, or wholly or partially across a river, or crossing floodplain areas to direct the passage of fish or to trap them. These structures can be made of earth, stone, or wood. Here, with a focus on storage processes, we will pay attention to structures that, in addition to allowing capture, provide some type of maintenance of animals for a period of time. The first mentions of weirs in the interior of South America are

in Llanos de Mojos, Bolivia (Hissink and Hahn, 2000) (savanna). (15) Modern wooden fish weirs constructed seasonally by the Enanewe-Nawe in tributaries of the Juruena River, Brazil (Mendes dos Santos and Santos, 2008) (uplands-savanna transition). (16) Ponds dug at springs and in stream channels at the Cipoal do Aaticum archaeological site, Trombetas River, Brazil: ~AD 900 to AD 1400 (Schmidt et al., 2014) (uplands). (17) Canals and ponds recorded at the Laguinho archaeological site, in the Central Amazon, Brazil: ~ AD 600 to AD 1100 (Schmidt et al., 2014) (floodplain). (18) Dams, reservoirs, and ponds observed while conducting fieldwork in the Upper Xingu that await mapping and dating (Schmidt et al., 2014) (savanna).



Figure 2. Fishing with cotton nets in an artificial pond. Baures, Bolivia (Credits: Franciska Reidel).

from the Baures region, Bolivia. In the extensive floodplain savannas of this region, Erickson (2000) identified kilometers of zigzag lines built of the earth (1 to 2 m wide and 20 to 50 cm tall). At the end of the savanna's flood period, these would help to block and direct the water. These structures were interpreted as fish weirs. More recently, Blatrix et al. (2018) have shown that these earth structures are spatially associated with artificial ponds.

In other areas of the Amazon, archaeological and historical accounts recognize similar waterworks (e.g., canals), yet their relation to fishing activity remains unresolved. As with the artificial river obstructions in the Upper Xingu (Heckenberger et al., 2003) that have been in use since the occupation of the area in AD 1200, the relation to fishing is unclear. In the Venezuelan llanos, Zucchi (1984) defined channel-like structures that connect rivers as "dikes," dated from AD 500 to AD 1400 (see Figure 1(1)). He maintains that the purpose of these constructions was to retain aquatic fauna, but no direct archaeological study has contributed to the understanding of their true function.

In the early 20th century, Nimuendajú (2004) toured the Lower Madeira River and described river dams in Rio Pretó do Pantaleaõ and in Lake Mastro (Brazil), which that author considers to be fish dams. Contemporary inland dam use does not reflect what is seen in the archaeological record. For instance, contemporary dams made by the Tacana group of the Llanos de Mojos (Bolivia) consist of stone and earth. The Tacana plug streams and small rivers with stone and clay dikes or put a double row of reeds at the bottom of the river (Hissink and Hahn, 2000). There are many references to wooden dams built specifically for fishing that are mentioned in the ethnohistorical record among

various indigenous groups in the Amazon. Well known are the fish dams made by the Enawenê-Nawê, who live in a transition region between the Cerrado and the Tropical Forest in the south of the Brazilian Amazon. Between February and April, the ceremonial practice of building the Enawenê-Nawê dam (*waity*) sees a collective mobilization and participation of the men who build it and live nearby for the duration of the project (Mendes dos Santos and Santos, 2008). These dams are built during the receding waters in rivers, when the fish leave the flooded areas and migrate to the river channels (see Figure 3).

Cacuris or fish corrals

Cacuris are traps to catch fish and keep them alive, like in corrals, which are used throughout Amazonia (Veríssimo, 1970; Silva, 2011; Cabalzar and Candotti, 2014). Two kinds of *cacuris* have a long history of use and are still used today: one portable and the other stationary. The stationary version of the trap is built at the edges of rapids or falls, in sections of the river where the water current flows over rocky outcrops, forming waves and swirls (Cabalzar and Candotti, 2014, p. 84). Silva (2011, p. 153) writes, "It is placed at the beginning of the flood (...) capturing in great quantity the shoals (*Leporinus* spp., *Curimata* spp. and *Pimelodus* spp.) that go upstream against the current during the food migrations."

On the other hand, the portable *cacuri* is considered a smaller variation of the stationary *cacuri* that is used to catch small fish. The fish enter through a hole, attracted by food (mainly termites), which floats in the inner surface of the artifact (Cabalzar and Candotti, 2014, p. 76). This trap is placed near the riverbank (Cabalzar and Candotti, 2014). Silva (2011)

described the use of *cacuri* to capture chelonians in places with fruit-bearing palm trees (*Mauritia flexuosa*) located near the headwaters of the Rio Negro.

Management practices that do not imply the elaboration of physical structures

Important to point out that, while forest people likely practiced aquatic animal husbandry, it is not inherent that a group will construct an edifice to maintain species for later consumption (Veríssimo, 1970). It is known that forest people use manioc root submerged in water to attract turtles and make them "accustomed" to this procedure over several days, thereby facilitating their future handling (Barboza et al., 2013). Littoral Amazonian groups describe microhabitats on the edge of the estuary as *emburateua* that serve to shelter fish to feed and reproduce. The *emburateuas*, whether artificial or natural, are characterized by fallen debris from mangrove trees and represent important fishing spots (Barboza and Pezzuti, 2011). A further example of husbandry devoid of special structures is offered by the Katukina indigenous people in western Amazonia, who are known to keep turtles temporarily tied and



Figure 3. Enawene-Nawe fish weirs (Mato Grosso) (Credits: Gilton Mendes dos Santos).

maintained in puddles or in home gardens for subsequent consumption (M. Barboza, personal observation). Although turtles are kept for short periods, generally a few days, they can be fed by people in natural environments without the need for any kind of structure.

Final Considerations

In this paper, we have presented a set of archaeological, historical, and ethnographic data that confirm aquatic environments as places of domestication scenarios. The structures built for the provisioning and captivity of animals seem to be planned using a deep knowledge of the diversity and plurality of Amazonian aquatic and terrestrial microenvironments, seasonality (water regime), land topography, quality and availability of constructive materials, and animal ecology (feeding) and behavior (trophic and reproductive migration, social interaction).

The archaeological ponds found in the Amazon region appear mainly in the seasonally flooded regions, such as the Venezuelan (Llanos Venezolanos) and Bolivian (Llanos de Mojos) savannas. The ponds that have been excavated so far in Amazonia have ranged from 12 to 38 m in diameter and from 1 to 2.5 m in depth. The water supply of these ponds could be linked to the flooding of rivers, as in the Baures systems, or precipitation such as at Loma Salvatierra and the Belterra Plateau. The function of these ponds seems to be linked to water dynamics. Perhaps they were built during the dry season—4 to 5 mo—as they can flood and retain water during the wet season. In some cases, as at Loma Salvatierra, channels ran from the highest to the lowest places, feeding the ponds with water.

Although absolute radiometric dates are not available for any of these structures, in Bolivian Amazonia, the oldest are dated to AD 300. The function of the ponds is not always clear. In Central Amazonia (Lago do Limão site), where stake marks were found, it is possible that they served as corrals for turtles. At the Belterra Plateau, interviews with contemporary residents near the archaeological sites indicate that the ponds are multifunctional. They are currently used for water supply, fish farming, and even for the introduction of other aquatic animals, such as alligators and turtles. Several features in the same site can work together as a system, and that the same structure might have more than one function. As for dam systems, there is diversity in the building material, wood, stone, or earth, but only earth and stone dams are visible in the archaeological record. Modern examples of *emburateua* and the current use of archaeological ponds in Marajó and Llanos de Mojos also demonstrate the use of traditional ecological knowledge for management strategies.

The duration of animal "captivity" and the period during which ponds can store fish is likely to show great variation. Duration seems to be quite variable depending on the structure, ranging from days to months. For example, although it is difficult to precisely affirm, we postulate that dams built of wood in rivers may only be viable for a few weeks or months. On the other hand, ponds can store fish throughout the drought period, depending on multiple factors such as the rainfall, flooding regimes, and fish taxa involved. Historical accounts suggest that turtles were stored in corrals for weeks or up to 1 yr. Thus, the structures related to the captivity of fish and turtles in the Amazon raise questions about the connection between a level of animal husbandry and the anthropogenically modified terrain, which we have termed waterscapes.

If a "classic" model of animal domestication did not occur in the Amazon, in terms of reproduction and length of captivity, clearly different cases of aquatic environmental management have existed over time in the Amazon. As suggested in the paper, some interventions and controls performed in aquatic environments depend more on daily observation and on the knowledge of the dynamics of these environments than in fact on a transformative physical intervention of the place. In these cases, it would be difficult to accurately classify the degrees of intensity. Even so, in some of the examples, as in the cases of the Baures region or the Marajó island, waterscape domestication allowed populations to permanently transform environments that would be seasonally or completely flooded or completely dry. Waterscape domestication allowed these populations to live out of water in flooded environments and to continue to manage water and aquatic fauna in periods that would naturally be absent. Therefore, perhaps what we are able to observe more accurately is the persistence of some changes over time.

The domestication that could appear to be "incomplete" from a western point of view seems to have been intentional, through a more in-depth, integrated, and engaged ontology. An example of this is indigenous perception of intangible beings—animals, plants, stones, spirits, etc. (Viveiros de Castro, 1998). Thus, the action of managing these environments also involves negotiating, collaboration, respect, and experimentation with multiple beings and the spaces they inhabit across time (Mendes dos Santos and Santos, 2008; Barboza et al., 2021). In this text, we have argued for the dialogue between waterscapes and associated parts (humans, tangible, and intangible beings). We further argued for the role of waterscapes in the archaeological and historical past on the ongoing building of Amazonian landscapes.

Evidence of water-managed structures are scattered throughout the archaeological and historical record; therefore, it will be important for the relationship between people and the Amazon that previous water technologies are revisited and systematically studied. To recognize the living memory of the people who built the forest, researchers need to understand the dimension of the waterscape. This is possible knowing the beings that inhabit it, the dynamics of their interaction, and the social complexity of human interactions with the environment and other beings. Most important is working with local people, who embody the deep socio-ecological knowledge of

About the Authors

Gabriela Prestes-Carneiro (PhD) is an assistant professor in the Anthropology and Archaeology Department at the Federal University of Western Pará State (UFOPA), in Santarém, Brazil. She is an Amazonian zooarchaeologist who has worked on archaeological shell mounds, anthropogenic dark earths, and monumental mounds in different regions of the Brazilian and Bolivian Amazon. Fish remains have been her primary specialty as she explores histories of the human use of the aquatic environments, subsistence changes, and

their relationships to the paleoenvironment. Corresponding author: gabi_prestes@hotmail.com

Roberta Sá Leitão Barboza (PhD) is a biologist specialized in Aquatic and Fish Ecology at the Federal University of Pará (UFPA) and has been working in the Amazon with artisanal fishermen since 2004 and teaching as a university professor for over 10 yr (UFPA). Roberta has developed studies on the uses, fishing, and community management of turtles in Amazon. Since 2014, she coordinates the research group Coastal Socio-

Environmental Studies and the Laboratory of Teaching, Research and Fisheries Extension for Amazonian Communities. Currently, she develops scientific studies (Fishermen's Social Organization, Local Ecological Knowledge, and Participative Management of Natural Resources) and scientific dissemination products for traditional communities in the Amazon.

Myrian Sá Leitão Barboza (PhD) is a biologist specialized in Cultural Anthropology and Latin-American Studies (University of Florida) and has been working in Amazonia since 2004. She has been an assistant professor at the Federal University of Western Pará State (UFOPA), in Santarém,

Brazil, for over 10 yr, where she currently coordinates the Archaeology course. She has experience with ecological, ethnoecological, and ethnographic fieldwork with different groups (indigenous, Afro-Brazilian, riverine, women, and social movements) in Brazilian Amazonia and the Northeast. Currently, Myrian is engaged with local communities on studies about past and present diets, community use and management of animal and plant resources, and gendered use of territory. Claide de Paula Moraes (PhD) is a professor of Archeology at the Federal University of Western Pará. He has experience in Amazonian Archeology, active mainly in the following research themes: peopling of the Americas, the year AD 1000 in the Amazon, the study of ceramic sites, study of lithic technology, indigenous people and archaeology, and teaching of archeology.

Philippe Béarez (PhD) is an archaeozoologist specialized in the study of interactions between humans and aquatic environments over time. Fish are his favorite animal group, which he studies in several ways: archaeoichthyology, anatomy, taxonomy, biogeography, and conservation. He is also interested in historical ecology and human impacts on aquatic ecosystems. He carries out archaeological work in South America (east coast of the Pacific, Amazonia), in the Indian Ocean (Arabian Sea coast), in Oceania (Melanesia and Polynesia), and in France.

Amazonia. These collaborative efforts will help identify which traditional methods can persist in the future and can be useful to deal with current problems resulting from unsustainable practices (Krenak, 2019).

Acknowledgments

We would like to thank the colleagues who kindly provided photos for use in this paper, namely, Gilton Mendes dos Santos, Leonor Rodrigues, Franciska Reidel, and Joana Troufflard. We thank the editors for their invitation to participate in this special issue. We are very grateful to Ney Rafael for helping with the map and Morgan Schmidt and Myrtle Pearl Shock for valuable information about their research in the Amazon. We are grateful to Kevin McDaniel and to the anonymous reviewers for the English proofreading of this paper and their constructive comments. We greatly appreciated the support and kindness of local people during our fieldwork conducted in Amazonia over the last 17 yr.

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CSAS Society News

President's Message

Despite this unprecedented Covid-19 pandemic, the Canadian Society of Animal Science is working diligently to support high quality animal research. CSAS is organizing two virtual symposia in collaboration with the American Society of Animal Science for the 2021 ASAS-CSAS-SSASAS Annual Meeting & Trade Show on the prospects for exploiting epigenetic effects in Livestock Production and livestock resilience and climate change. In addition, the CSAS in working on the November issue of Animal Frontiers, showcasing how epigenetics will impact livestock production in the future with contributions from authors that will provide a global perspective. We hope these events and publications will contribute to the scientific community and animal production stakeholders.

For more information on the CSAS activities visit our LinkedIn page at https://ca.linkedin.com/company/ canadian-society-animal-science.

Best wishes,

Flavio S. Schenkel (President), on behalf of the Canadian Society of Animal Science Executive



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THE 72nd EAAP ANNUAL MEETING WILL BE HELD IN DAVOS (SWITZERLAND)

EAAP and the Swiss Local Organizing Committee for the 2021 EAAP Annual Meeting wish to inform you that, despite the trouble caused by the Covid-19 pandemic, the 2021 Annual Meeting will be held from 30th of August to 3rd of September, as originally planned. The structure of the meeting depends on future pandemic developments and the related governmental restrictions. The option that we are currently considering is to hold a hybrid meeting, that is to have an on-site meeting in Davos with selected sessions offered virtually. The Theme of the conference will be: "Scientific solutions to different demands on the livestock sector".

The Annual Meeting will host scientists and experts from all disciplines of animal science. The EAAP Meeting provides a platform for scientists and industry experts to meet and acquire new knowledge and to exchange their experiences on the latest research results from many areas of animal science. The Plenary Session this year is titled "The multiple roles of livestock in sustainable development ".

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More information can be found at www.eaap.org and the Congress website www.eaap2021.org

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